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PROCEEDINGS OF
THE LINNEAN SOCIETY OF LONDON
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PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

Session 1952-53

Vol. 165

Part 1

PROCEEDINGS OF THE GENERAL MEETING, 9 October 1952

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the Anniversary Meeting held on Saturday, 24 May 1952, having been circulated, were taken as read, and confirmed.

The following letter from the Keeper of the Privy Purse and the Loyal Address in reply, were read by the PRESIDENT :—

Privy Purse Office,
Buckingham Palace.
22nd July, 1952.

Dear Sir,

I am commanded by The Queen to inform you that Her Majesty has been graciously pleased to grant her Patronage to The Linnean Society of London.

It will be in order for the words " Patron—Her Majesty The Queen " to appear in future under the name of your Society on all correspondence.

Yours truly,

ULICK ALEXANDER,
Keeper of the Privy Purse.

The President,
The Linnean Society of London,
Burlington House,
Piccadilly, W.1.

To the Queen's Most Excellent Majesty.

THE HUMBLE ADDRESS OF THE PRESIDENT, COUNCIL, AND
FELLOWS OF THE LINNEAN SOCIETY OF LONDON.

May it please Your Majesty,

We, the President, Council, and Fellows of The Linnean Society of London in General Meeting assembled, wish to express our Loyalty and very deep devotion to your Majesty's Person, and pray that your Majesty's Reign may be long and distinguished.

The Society is deeply appreciative of your Majesty's gracious consent to continue the practice of your Predecessors by becoming Patron of the Society.

Given under the Common Seal of the Society, this ninth day of October in the year One thousand nine hundred and fifty-two.

L. S.

R. B. SEYMOUR SEWELL, *President.*

F. C. STERN, *Treasurer.*

A. TINDELL HOPWOOD, } *Secretaries.*
GEORGE TAYLOR, }

The following were thanked for gifts made to the Library since the last Meeting :—Dr. F. Børgesen, Miss M. H. Chambers, Dr. Philippa C. Esdaile, Mr. H. E. Hammond, Mr. R. H. Hooper, Mr. H. A. Hyde, Miss D. J. Jackson, Dr. Jaime Jaramillo-Arango, Mr. Charles McCann, Mr. R. D. MacLeod, Mr. O. B. Miller, I.S.O., Dr. R. G. Newton, Mr. A. A. Prestwich, Dr. G. Rudolf, Sir Edward Salisbury, C.B.E., F.R.S., Miss R. F. Shove, and Messrs. Methuen & Co. Ltd.

The following signed the Obligation in the Roll and Charter Book and were, admitted Fellows :—Dr. John Heslop-Harrison, Mr. John Patrick Micklethwait Brenan, M.A., Mr. Leonard Victor Hand Gingell, Dr. Margaret Elizabeth Brown, Miss Kathryn Benson-Evans, M.Sc., Professor Francisco D'Ascensão Mendonça and Dr. Owen Lynden Wade.

The PRESIDENT reported the death of Dr. William Thomas Calman, C.B., F.R.S., Fellow of the Society ; and moved the following Resolution, which was passed in silence, all present standing in their places :—

The Fellows of The Linnean Society of London having heard with the deepest sorrow of the death of Dr. WILLIAM THOMAS CALMAN, C.B., F.R.S., desire to place on record their high appreciation of the service he has rendered to the Society during the forty-five years of his Fellowship. Elected first in 1906, and after a short break, again in 1919, he served on the Council from 1913–16, 1922–29 and 1931–38. He acted as Zoological Secretary from 1923–28, was appointed Vice-President for 1928–29, 1933–34 and 1937–38, and held the office of President from 1934–37. Dr. Calman was awarded the Linnean Medal in 1949. During his long Fellowship of the Society he showed the greatest interest in its work, and until his retirement regularly attended its Meetings. Deploing the loss of so distinguished a Fellow, the Fellows desire to express to Mrs. Calman and her family their deep sympathy with them in their bereavement.

Certificates of recommendation for election to Fellowship were read for the first time in favour of the following :—David James Allott, B.Sc., Geoffrey Howard Banbury, B.Sc., A.L.S., Frederick Bond, John Wells Day, Francis John Fulton Fisher, M.Sc., Arthur Leslie Galliford, J. Donald Grose, Miss Joan Linnell Ivimy, Arthur John Juniper, B.Sc., William Henry Lomas, B.Sc., Clive A. Loos, Homai Jal Moos, B.A., M.Sc., Arthur Hoyle Parkinson, B.Sc., M.S., Ph.D., David Norman Paton, M.A., Robert John Pullen, William Alfred Rainford, and Jacob Seide, M.D., Ph.D.

A colour film and slides of the Falkland Islands and the Antarctic were shown by Dr. William J. L. Sladen, M.B.E., who also gave a commentary. The slides and film illustrated the work being carried out by the Falkland Islands Dependencies Survey, the voyage on the Survey Vessel "John Biscoe", and the fauna and flora of the Falklands and Dependencies. (Discussed by Dr. N. A. Mackintosh and Dr. Julian Huxley ; Dr. Sladen replied.)

**PROCEEDINGS OF THE GENERAL MEETING,
23 October 1952**

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 9 October 1952, having been circulated, were taken as read, and confirmed.

The PRESIDENT read a letter from the Assistant Keeper of the Privy Purse expressing Her Majesty The Queen's thanks for the Loyal Message sent on 9 October 1952.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. P. E. P. Deraniyagala and Professor Erland Ehrmark.

The following signed the Obligation in the Roll and Charter Book, and was admitted a Fellow :—Patrick Joseph Lindsay Roche, L.R.C.P.

Certificates of recommendation for election to ordinary Associateship were read for the first time in favour of the following :—Donald William Brett, John Greenland Hughes, B.Sc., Eric Cartwright Jones, B.Sc., and Miss Joana Mary Kain ; and certificates of recommendation for election to Fellowship were read for the second time in favour of those candidates whose names appear in the Minutes of the Meeting held on 9 October 1952.

A Discussion on the Classification of Fungi was opened by Dr. B. Barnes, Mr. E. J. H. Corner and Dr. J. Ramsbottom, O.B.E.

In the general discussion the following took part :—the President, Professor C. T. Ingold, Miss E. M. Wakefield, O.B.E., Mr. W. E. Hollows and Dr. E. M. Delf ; Dr. Barnes, Mr. Corner and Dr. Ramsbottom replied.

THE CLASSIFICATION OF THE LOWER FUNGI

By Dr. B. BARNES.

It does not seem necessary to question the prevailing view that the Phycomycetes include the simplest-known fungi, but there is no reason to think that they have algal affinities. The characters of the thallus, and the number of flagellae borne by mobile stages, appear to provide good guides for the main lines of classification within the group. The most simply organized Phycomycetes (to be found in the Chytridiales and at the base of the Saprolegniales) have likenesses to the Monadineae zoosporeae, and it is probable that the Phycomycetes have developed from creatures of that level of organization. Tendencies which can be discerned among the Monadineae zoosporeae become more developed and specialized in some of the sub-groups of the Phycomycetes which have filamentous thalli, though we do not seem as yet to have noted tendencies which link the Zygomycetes to the other Phycomycetes, nor the Phycomycetes to the Ascomycetes and Basidiomycetes.

Speculation on the classification and on the possible relationships of the Phycomycetes must be limited to a consideration of tendencies. It is idle to attempt to arrange the existing species in phylogenetic trees.

THE CLASSIFICATION OF THE HIGHER FUNGI

By E. J. H. CORNER, M.A., F.L.S.
Botany School, Cambridge.

Classification in biology has two purposes. One is to name the organisms, for which any short cut may be suitable. The other is to relate the organisms scientifically in the natural scheme of things, and for this there is only the evolutionary method. It may be convenient for identification to classify whales with fish, cacti with euphorbias, or noxious bacteria with noxious insects, but such artificial groups will frustrate scientific research. Consider the muddle for the morphologist, physiologist, or geneticist, if *Ranunculus*, *Potentilla*, *Dillenia* and *Ochna* were placed in one family because of their general floral resemblance. *Ranunculus* is a ranunculaceous problem, *Potentilla* a rosaceous, and so on. It is the duty of taxonomists, as it has been the progress of taxonomy, to discover phylogenetic groups: mis-alliances obscure research. That is why I regard fundamental taxonomy as the pivot of biology.

Simple as this seems, it is very often forgotten. The attempt to consider the evolution of organisms and to disentangle phylogenetic resemblances from homoplastic or convergent is frequently condemned as speculation. Now, I have seen monkeys identify with grimace and chatter as accurately as I could with scientific keys. It is contemplation that raises us above the beast. This very speculation is the ignition of taxonomy. Dull the mirror, or stop the look-out, and taxonomy is lifeless. Indeed, general botany seems quite unaware of the critical weapon of research which fundamental, and phylogenetic, taxonomy has placed at its disposal. Text-books abound in generalizations drawn from plants of most diverse affinity. From *Spirogyra* we pass to *Fucus*, *Mucor*, *Agaricus*, and so on to the sunflower and grass, mistaking analogy for homology. This loose method of comparison becomes the student's habit and neither he nor his teachers seem to know that, in the vast accumulation of taxonomic research, lies the corrective. The natural term of biological enquiry is the genus, to be extended to the tribe and family, and not until these extensive researches have been made can we really see what the grass has to tell the pine, or the mushroom the mould. Such is the precision of taxonomy.

Now, the classification of the higher Basidiomycetes is extremely backward: it is too artificial for scientific research: often it is too superficial even for identification. There is a mushroom-grade, the Agaricaceae, as if shrubs or laminate seaweeds or saprophytic flowering plants were placed in one family. There is a polypore-grade, a hydnum-grade, and so on, which may be likened to the Apetalae or Metachlamydeae among the artificial grades of flowering plants. The puffball-grade, the Gasteromycetes, is like a taxon for tubers. So little emerges from these grades or mixtures, that I am not surprised the subject is irksome for teachers. In contrast, the physiology, biochemistry, genetics and ecology of the same fungi are lively topics. I venture, therefore, to offer a phyletic approach to their classification which will introduce the speculation needed for research.

A higher fungus consists of a vegetative mycelium and a spore-producing fruit-body. The mycelium is so little diversified structurally that it does not offer yet a means of classification: it is comparable with the root-system of land-plants, but its simplicity is more probably the result of efficiency than of primitiveness. Classification depends on the great diversity of the fruit-body. What has been its evolution? This is the problem that the taxonomist must face.

What is a mushroom? It looks very like an umbrella, even with a ring. Buller's researches have shown it to be a very precise mechanism for spore-

production. If a piece of a gill is examined alive in a moist chamber, as Buller did, one can see all the delights of his sporobolistics. But, immerse that piece of gill in water, as he rarely did, and very soon all the cells which are developing spores will collapse, and no more will be formed. Water, and other liquids, cause the apex of the basidium with its sterigmata to collapse, for which reason drawings of basidia generally show distorted sterigmata: yet, they are the needles of the mechanism. I conclude that a mushroom is an umbrella, which keeps the rain off the gills while these operate moist chambers. Similarly a polypore is a shelf that keeps the underside dry and yet maintains the humidity in the honey-comb where the spores are forming. How different is the ascomycete which develops its spores under water in the hymenial mucilage, and which goes in for cups and little flasks which hold water! Nothing so simple can creep into our sophisticated text-books, and so the student never gets the hang of these two kinds of higher, or larger, fungi, so diametrically opposed in their fruit-body mechanism. The student is even lead to believe in jumping from *Peziza* to *Agaricus*, as one might hop from London to Paris, that the basidiomycete has evolved from the ascomycete.

Now, one grade of these Basidiomycetes does not have the developing spores protected from the rain. It comprises the clavarias, whose club-shaped or coral-like fruit-bodies must therefore be regarded as the least perfected and the less evolved. They do not keep their spores dry, and so collapsed tetrads of immature spores are very often to be seen on their surfaces. I find it impossible to believe that any other kind of Basidiomycete, with its spore-surface facing neatly down or in, could have turned it up to the splashing that a clavaria gets, and have survived in nature. It is my hypothesis, therefore, that the clavaria fruit-body is the start for the evolution of higher Basidiomycetes: and, accordingly, I approached their classification.

I found that, microscopically, there were six ways at least of making so simple a structure as a club-shaped fruit-body. These ways distinguished natural genera, or natural groups of genera, in the world-flora: that is, the classification was definite because it revealed absolute distinctions, instead of the vague boundaries of an artificial system. One of the groups is pre-eminently instructive, because it shows that the Clavariaceae are an artificial grade of genera with similarly shaped fruit-bodies, and not a phylogenetic unit. The particular group consists of the two tropical genera *Lachnocladium* and *Clavariachaete*. They agree in all microscopical details, not with other Clavariaceae, but with the yellow-brown species of Polyporaceae, Thelephoraceae, and Hydnaceae. In the British flora, *Polyporus hispidus*, *Fomes igniarius*, *Hymenochaete* and *Asterostroma* belong in the alliance, and have no near affinity with such as *Polyporus squamosus*, *Fomes fomentarius*, *Stereum* or *Corticium*. *Lachnocladium* and *Clavariachaete*, indeed, show a fundamental dichotomy of the alliance into two divisions, one with dichophyses and the other without. *Hymenochaete* is a mixture of both kinds and represents a stereum-grade of the series: *Hymenochaete* thus needs complete microscopic analysis before it can be useful to scientific research.

This great alliance of species with yellow-brown fruit-bodies I call the 'Xanthochroic series', because I have no idea whether it is a primary, secondary, tertiary or lesser subdivision of the Basidiomycetes. It cuts across the artificial grades of present-day classification, even picking species from subgenera. It shows how the form of the fruit-body has evolved from the clavarioid to the stereoid, hydroid and polyporoid, while retaining its characteristic microscopic construction. Thereby it shows how the classification of these higher Basidiomycetes must be entirely re-set before it can have the necessary precision. On the old system, *Lachnocladium* was simply a jumble of any branched tropical clavarioid fungus, even if it were a pyrenomycete, and no investigator could make head or tail of such confusion until the

classification had been scientifically rectified. I repeat that I do not wonder such stuff cannot be taught.

In the Xanthochroic series the hyphae rather quickly develop thick walls, thus preventing the evolution of the mushroom habit which depends on inflation of the cells to open the umbrella. Another clavarioid series, however, that of *Clavariadelphus*, leads to *Cantharellus*, but, as the Cantharellaceae are a muddled grade of diverse phylogenetic series, it is impossible as yet to know if it leads to true agarics. I suspect not. The *Ramaria*-series of clavarioid fungi leads to a different group of cantharelloid and stereoid fungi. The *Thelephora*-series leads on to some hydroid fungi: the *Pterula*-series leads to yet others. Only the *Clavaria*-series itself stands apparently unconnected.

It will be understood now that world-monographs of these various grades must firstly be undertaken to dissect them into natural units, and then these units can be pieced together in phylogenetic series. There is nothing cryptic or speculative about such straightforward microscopic anatomy.

I will mention three other examples—*Fomes*, the puffballs and *Corticium*. In Britain there are three large brown polypores of similar appearance, namely *Fomes applanatus*, *F. fomentarius* and *F. igniarius*. In each one, however, the microscopic structure is so different and connects, in each case, with so many other kinds of polypore, that each represents a family, rather than a species of a genus. *Fomes applanatus* is nowadays put into *Ganoderma* but this genus is ranged alongside of *Fomes*. Actually, *F. igniarius* is more closely related to *Clavariachaete*, represented by two species from tropical America, than it is to either *F. applanatus* or *F. fomentarius*. Our present treatment of these polypores is so superficial that it is not merely as if a cactus, a euphorbia and an asclepiad had been put in one genus, but like the early days of algology before the microscope had sorted out the red and brown seaweeds.

Following the hypothesis that the *Clavaria*-form is the primitive, an end-product will be the puffballs, or Gasteromycetes, with the hymenium completely internal. *Ex hypothesi*, the group consists of the end-products of many lines of evolution, and is thus a grade of convergence comparable with the truffles and *Elaphomyces*. It is, in fact, now being discovered that some of these Gasteromycetes are to be related with diverse agaric-genera as *Russula*, *Psalliota*, *Cortinarius*, *Boletus* and others. The discoveries are based on microscopic anatomy, exactly as with the Clavariaceae and *Fomes*. Yet, it is a current opinion that the Gasteromycetes are a starting point for the evolution of other forms of Basidiomycete. There is, in fact, a morphological series which can be read in either direction. That is why I consider the mechanism of spore-discharge to be 'time's arrow', pointing to, not from, the puffball.

The most difficult group to evaluate will be that of the resupinate Thelephoraceae, exemplified by *Corticium*. The fruit-bodies consist practically of a layer of basidia on the underside of organic débris. *Ex hypothesi*, they are derived from bracket and pileate forms from which all the form-factors of the fruit-body have most economically disappeared, except for the positively geotropic, rain-protected hymenium. *Ex hypothesi*, the resupinate Thelephoraceae are a mixture of all lines of Basidiomycetes that have reached this state of efficiency. Some are easily separable as Tremellales and Auriculariales: others are referable to clavarioid series, as to the Xanthochroic and the *Thelephora*-series itself; and yet others have hydroid affinities. I have found, too, that the clavarioid *Pterula* can form resupinate fructifications. I doubt, therefore, that this grade can be deciphered until the so-called higher Basidiomycetes have been interpreted phylogenetically.

In conclusion, I would say that the Xanthochroic series is the only extensive phyletic series that is known among the Homobasidiomycetes. There is a most exciting field of research to discover the others.

THE CLASSIFICATION OF FUNGI—GENERAL CONCLUSIONS

By Dr. J. RAMSBOTTOM, O.B.E.

Calling to mind remarks made by Huxley and by Osler I feel that probably my contribution to this evening's discussion needs the justification that I accepted the invitation because my ideas about the classification of fungi are as confused as they were about forty years ago—perhaps worse confounded.

We have had two special aspects of the problems put before us; I shall be more general.

Broadly speaking the two main objects of classification are the identification of organisms, and their arrangement in a scheme, or possibly schemes, to show their relationships. I have been forced to the conclusion that to do either of these satisfactorily, regard must be paid to the nature of the organisms. To those impatient of the niceties of mycological taxonomy I was wont to suggest that it was no part of the work of a systematist to have searched out the recondite details which an investigator discovered in his own researches though these should be taken into account both in identification and classification; a sort of 'give us the tools and we will finish the job'.

No one having to deal with the various strains of fungal species causing disease, or used in industry, would be able to classify them without regard to the differences shown in their physiology and chemistry. It is not suggested that a systematist must study these matters at first hand but that he should take them into account when speculating on his problems, as he must do in his practice. An interpolation on classification may not be out of place. Fungi may be 'classified' in all sorts of ways following the example of Dioscorides—fungi which are edible, and fungi which are poisonous. All who study fungi for any particular purpose have some such grouping in mind; species with large nuclei; which destroy timber; which cause disease in plant, insect or man; which ferment sugars—and so on. Such are in their last terms often invaluable aids to identification, and correct identification is the foundation on which all superstructures must be built. Keys—so-called artificial keys—if with sufficient details are of the same type, though usually these are so meagre that only an approximation is possible. In herbaria, 'classification' is mainly with the object of finding a given specimen with the least trouble. It is for this reason that in large herbaria Saccardo's *Sylloge Fungorum* is used, as it has as its aim the description of all species; it is a calamity that no volume has been published since 1931. For small areas such as counties or countries any existing local flora suffices. Monographic studies of genera or families are sometimes used when available, but it is obvious that a purely alphabetical arrangement would serve, as it does for odd species not treated in Saccardo.

So soon as culture methods got into their stride many odd facts came to light, though not of the kind that were announced with such confidence before the restrictions of purity were realized and accepted. The ancient uses of yeasts for fermenting were subjected to a new scrutiny with such thoroughness that with the possible exception of ergot (*Claviceps purpurea*), and now of *Penicillium*, they rank first amongst the fungi whose chemistry and physiology have been properly studied. But the morphology of yeasts offers little scope for morphological distinction and identification methods were evolved which rely mainly on cultural characteristics, principally the fermentation of different sugars.

During the past half century cultural methods have revealed that many species which can be grown on media consist of numerous strains which can be isolated and remain true to type. Further, that there are often mutations, or saltations, shown frequently as sectors, and these often remain true in culture.

A parallel phenomenon occurs in specialized parasitism. It is best known in Rusts where it was first recorded by Schroeter in *Puccinia graminis* in 1874 : our real knowledge, however, dates from Eriksson's work in 1894. The so-called 'biological species', 'biological races', 'physiological species', 'physiological races' are difficult to assess taxonomically. The problem may be gauged by the fact that there are twelve of these forms in *Puccinia graminis* and that what have been called biotypes have been recorded in the six most common. Stakman and his co-workers had isolated thirty-seven by 1929 ; as these can arise both by mutation and by intercrossing there seems no end to the possibilities. Thus Race 15 was discovered in 1918—all except one of the twelve differential varieties of wheat used for testing were susceptible. A second biotype 15A was obtained from a Japanese collection. In 1937 a third biotype 15B was discovered ; in 1939 it was recorded from Barberry (the alternate host). In 1950, Race 15B destroyed 10 million bushels of durum wheat in U.S.A., about one-fifth of the crop ; fortunately that year bread-wheat varieties matured before the disease reached epidemic proportions—it is the most virulent race of Black Rust ever found in North America. No commercial variety of wheat is immune. Presumably it arose by natural hybridization on the Barberry and suddenly became rampant in fifteen States on man-produced wheat hybrids.

Along with these we have the development of the penicillin story. After it was found that Fleming's strain of *Penicillium notatum* did not grow satisfactorily in submerged culture the National Research Laboratory at Peoria had collections of soil and mouldy products collected all over the world by the Air Transport Service—and the most profitable strain was sent in by a Peoria housewife on a mouldy cantaloupe she had bought in the local market.

By selecting strains and variants induced by X-rays and ultra-violet light the production of approximately 2 units of penicillin per millilitre of Fleming's original strain in surface culture has been boosted up to more than 1500 units.

How are we to treat strains such as those of Rusts and those of *Penicillium notatum-chrysogenum* ? It is useless to say that they are no concern of the taxonomist, whether occurring naturally or induced in the laboratory. The importance of the one in destroying food and of the other in combatting human disease gives the answer to those of us who, when these problems were not so pressing, tended to side-track them. The unit of classification is the individual.

The search for antibiotics—a wretched term that apparently has come to stay—has not led to the possibility of defining species or strains by their products in culture. Though the *Penicillium notatum-chrysogenum* group produce penicillin in the largest amount other species and other genera also do so, and, further, five natural penicillins are known. It is worth remarking that mycology and biochemistry are not synonymous ; biochemists had this impressed upon them during the war, but some mycologists have yet to learn that the reactions of a fungus in culture are not necessarily physiologically cut and dried.

In recent years great stress has been laid on what are termed chemical reactions in the larger fungi, especially in trying to differentiate species of *Russula*. Rolland started the ball rolling in 1887 and twenty years later Arnould and Goris showed that the flesh of species of *Russula* and *Lactarius* often has characteristic colour changes when touched with a drop of sulphovanillin or sulphoformalin. Since then a phallanx of chemical solutions has been employed. Many of them are very useful but they are empirical and should be regarded as adjuncts in diagnosis, not as specific characters. Many mycologists rely almost entirely on ferrous sulphate for identifying the variable *Russula xerampelina*, which is thought to be the only species of the genus which shows a green coloration when so treated : it is not known what the reaction signifies or whether it takes place under all circumstances and at all ages.

We know little about variation in fleshy fungi. True, they are not amenable to the cultural discipline to which moulds so readily submit, but we are accustomed to lump together the numerous forms of *Laccaria laccata* into the species and var. *amethystina*. If the species were uncommon, doubtless some of the extreme forms would be treated as distinct species. Probably a detailed study of this common species would help to solve some of our problems and provide others. Is it common because it is variable, or variable because it is common?

Another abundant species, *Armillaria mellea*, has been studied from many aspects but there has been no real systematic investigation. What are the relations of the numerous growth-forms? What appears to be a ringless form, called in many books *Armillaria mellea* var. *tabescens*, is thought by some to be a *Clitocybe*. Just before the last war we grew the type and 'tabescens' in culture. Both formed rhizomorphs but only the 'tabescens' fruited, remaining true to type. It is certainly distinct, i.e. it is not a growth-form, but what is its relation, if any, to *Armillaria mellea* or to the rare *Clitocybe ectypa* of marshes? The presence or absence of a ring has great weight in the old classifications and is still regarded with respect in spite of *Amanita jurgullea* occurring both with one and without.

The usual divisions of the Agarics are based on gross morphology and spore colour. The method has served mycologists well for about a century and will continue to do so. It is, however, artificial as it takes no account of development. We are in need of details of this and of the anatomy of the majority of species. There is here a little and there a little which can be made use of, but for the most part a ring (annulus) is a ring—or the remains of a cortina. If *Lepiota* is defined as having white spores, free gills, and a ring, we lump together a number of species which are not related, and leave out some that are. If the spores are green we have *Glaucospora* but often retain the wandering *achinata* with brownish then reddish spores—rejecting *Pholita aurea* with brown spores (though it has been made the type of the genus *Phaeolepiota*). Other species have cream coloured spores, some have pinkish. The logical method would be to group all the species together which show by their development and their anatomy that they are related, no matter what the colour of the spores or the mode of attachment of the gills.

Spore ornamentation is of considerable importance. That of *Russula* as worked out by Crawshaw might give phanerogamists hints in their study of pollen grains. Its importance in tracing phylogenies has been stressed, particularly by French mycologists, R. Heim in a series of erudite studies tracing various Gasteromycetes to series in *Russula* and *Lactarius*. If these views hold they upset such phylogenetic schemes as those of Cunningham who regards *Rhizopogon* as the primitive Gasteromycete genus and derives the others from it.

On the whole I regard phylogenetic lines at their best as interesting speculations rather than as realities; many which have been perpetrated are worthless except as tablets of remembrance for elementary students. When fungi had more scant treatment at the Universities even than at present, they were regarded as decadent algae and superficial similarities were listed to show from whence they originated. For over forty years I have been convinced that such ideas are without any foundation. I formed the opinion then that fungi were non-chlorophyllous from their beginning and this has remained one of my few convictions.

It is obvious that we have first to get a clear knowledge of details if any theorising is to be worth while. Thus, how could one explain the clamp-connections in the mould *Zygodesmus* and not elsewhere except in Basidiomycetes. The explanation is that *Zygodesmus* is a synonym of *Tremella* a Basidiomycete. Similar odd occurrences are always more worthy of study than of theory.

To return to the principles of classification : from the earliest times it was realized that some fungi are very similar—or related. The earliest groupings—or classifications—took note of this, sometimes indicating relationships by lines or by circles and many ideas were put forward to explain the supernatural principles underlying similarities. It was decidedly not the acceptance of the theory of evolution that justified the work of early systematists, for this was only a probable explanation of what were taken to be obvious affinities.

Nowadays the theory of evolution is a dogma which is never questioned, and therefore never really understood. How otherwise can we explain the disfigurement of our literature by the so-called phylogenetic trees knotted with modern genera, a sort of evolution in our time?

A phylogenetic classification presupposes that there has been evolution ; if reasonable, it suggests along what lines certain changes have occurred. Probable relations are mapped out and groupings made. Phylogeny can then assist in deciding which are probably the most primitive forms in a given group : groupings at end-lines add further problems. It must be realized that evolution cannot be both the key and the lock.

For myself I favour the view that, generally speaking, the simplest forms are presumably the most primitive and that reduction has occurred in only a few groups as, for example, yeasts.

What is a reasonable hypothesis of the factors influencing the evolution of fleshy fungi? The many strange forms seem to originate for the increase of spore-bearing surfaces, as against the need for photosynthesis influencing the shapes of flowering plants. Millions and millions of spores are produced and there appear to be special devices for their effective liberation and dispersal. What is the object of this prodigality? That the few shall be sure to fall on good ground! The production of such myriads of spores can hardly be an effective factor, for millions more or less would probably not affect the success of the species, and presumably this and this only is what really matters.

In my opinion the mycelium is often much more effective in reproduction. Very many species grow in rings which sometimes reach a great age. But systematists pay little regard to the mycelium even when underground strands or sclerotia are formed, though it is the mycelium which is ecologically important. Sclerotia are often distinguishable on microscopic characters, as Remsburg showed for those of *Typhula*, and is known also for those of the *Collybia tuberosa* group (*C. tuberosa*, *C. cirrhata* and *C. racemosa*) and of the Discomycete, *Sclerotinia*.

The hypha is the basis of all fruit-bodies. It becomes modified in various ways both in development and in relation to its activities. The structure of the enormously successful strands of *Merulius lacrymans* is worthy of study and reflection ; and those of *Armillaria mellea* in relation to its activities provide material for a consideration of form and function.

In my view all these niceties provide the real data which have to be considered in our theories of possible evolutionary tendencies. But we have to beware lest we overstress biological characters. Production of sclerotia, change in colour of the flesh, luminosity and such like occur in many fungi far apart in systematic position ; their importance, at most, is generic, is usually only specific but may be merely varietal. Thus the so-called predacious fungi, which attack eel-worms, rotifers, protozoa and even spring-tails, adopt methods much of a pattern, though there is an occasional spectacular diversion. At first sight they would appear to be closely related but most of them are either Mucorineae or Hyphomycetes, and one genus, *Nematochonus*, has clamp-connections.

Perhaps I might best summarize further remarks on these points by saying that in classification it is more important to decide what organisms are than what they do, though their activities be the reason which calls for certain identification.

**PROCEEDINGS OF THE GENERAL MEETING,
20 November 1952**

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 23 October 1952, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. A. E. Haarer, Dr. A. Tindell Hopwood, Mr. A. A. Prestwich and Col. F. C. Stern, O.B.E., M.C.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Mr. H. E. Goto, Mrs. Sybil Alice Stern and Mrs. Antoinette Nellie Gibby.

The PRESIDENT reported the death of Sir Frederick William Keeble, Kt., C.B.E., F.R.S., Fellow of the Society.

The PRESIDENT read a letter from Mrs. W. T. Calman, thanking the Fellows for their Resolution of Sympathy on the death of the late Dr. William Thomas Calman, C.B., F.R.S., F.L.S.

The following candidates for Fellowship and Ordinary Associateship were balloted for and elected. FELLOWS :—David James Allott, B.Sc., Geoffrey Howard Banbury, B.Sc., A.L.S., Frederick Bond, John Wells Day, Francis John Fulton Fisher, M.Sc., Arthur Leslie Galliford, J. Donald Grose, Miss Joan Linnell Ivimy, Arthur John Juniper, B.Sc., William Henry Lomas, B.Sc., Clive A. Loos, Homai Jal Moos, B.A., M.Sc., Arthur Hoyle Parkinson, B.Sc., M.S., Ph.D., David Norman Paton, M.A., Robert John Pullen, William Alfred Rainford, Jacob Seide, M.D., Ph.D. ORDINARY ASSOCIATES :—Donald William Brett, John Greenland Hughes, B.Sc., Eric Cartwright Jones, B.Sc., Miss Joana Mary Kain.

Two coloured films were exhibited :—

Miss Katherine Tousey of the Massachusetts Audubon Society, 'Audubon's America', and Dr. E. Schelpe, F.L.S., 'Vegetation in the Kangra Himalaya'. Miss Tousey and Dr. Schelpe commented on their respective films.

**PRESIDENT'S RECEPTION,
4 December 1952**

The PRESIDENT, Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., received the Guests in the Library.

A coloured film, 'Atlantic Seals on Ramsey Island', was shown by Asst. Professor H. R. HEWER, F.L.S., with a commentary.

EXHIBITS IN THE LIBRARY.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM. Photography of the sea floor. [Shown by Dr. H. G. VEVERS.]

The first attempts in this country to obtain representative samples of photographs in offshore waters as a means of estimating the density of

epifaunal invertebrates on the sea bed have been made at the Plymouth laboratory. The underwater photographic apparatus was designed to take 40–45 pictures of the sea floor at each lowering. The photographs displayed were obtained on the Plymouth trawling grounds in depths of 50–70 metres. They show a number of different marine animals in their natural surroundings and have already yielded interesting information on large concentrations of certain species.

In one area (south of Looe, in Cornwall) the photographs have shown a stationary population some miles in extent, with an average density of more than 100 individuals of the brittle-star *Ophiothrix fragilis* to the square mile. In a smaller area near the Eddystone there were about 340 individuals per square metre. This species of brittle-star feeds largely on suspended detritus brought to it by local water movements. From the economic standpoint this brittle-star is of negative importance, for although it is not eaten by fishes, its aggregations cover large areas of the sea bottom which might otherwise provide valuable feeding grounds for marketable fish.

CHELSEA POLYTECHNIC. Rhythmical activity in *Anodonta* (Freshwater Swan Mussel). [Shown by Mr. GORDON E. BARNES.]

The exhibit showed experiments and recordings demonstrating rhythmical activity in the adductor muscles of *Anodonta*. During periods of activity the shell valves are, at regular intervals, rapidly adducted and then allowed to return slowly to the gaping position. This 'rapid' rhythm has an average frequency of about 15 per hour. The periods of activity alternate with periods of quiescence during which the shells are held firmly closed. These alternating periods themselves occur rhythmically with a frequency which varies from one individual to another and which has a value of 3–30 per week. This has been termed the 'slow' rhythm.

The rapid rhythm is a function of the striated portion of the adductor muscles, and is under the control of the nearest ganglia (i.e. the cerebro-pleural ganglia at the anterior end, and the visceral ganglia at the posterior). The slow rhythm is brought about by the unstriated portion of the muscles under the control of the cerebro-pleural ganglia.

These rhythms are maintained independently of changes in oxygen tension, carbon dioxide tension, or food concentration in the external environment. The rapid rhythm is still exhibited by an animal that has been eviscerated, except for the visceral ganglia and the posterior adductor muscle.

In the intact animal the rapid rhythms of the adductor muscles are coordinated in such a way that every contraction of the posterior adductor has an anterior counterpart, but every contraction of the anterior adductor muscle does not have a posterior counterpart. If the cerebro-visceral connectives are cut, the synchronization is lost, and the muscles exhibit rhythmical contractions of different frequency.

FRESHWATER BIOLOGICAL ASSOCIATION, AMBLESIDE. The diatom genus *Tabellaria*. [Shown by Miss BRENDA M. KNUDSON.]

T. flocculosa is one of the commonest British freshwater diatoms, and the earliest known figure of it (*Philos. Trans.*, 1703) was exhibited together with live material at a similar magnification.

Photographs, drawings and microscopic preparations showed the various types of colony found in this genus, viz. 'zigzag', 'straight-line', 'star', 'corkscrew', 'parachute' and 'band'. The structure of the septa was also illustrated, and the frustule structure of *T. fenestrata*, where the dividing-cell always contains four septa, was contrasted with that of *T. flocculosa*, where the number of septa at cell-division increases with decrease in valve-length.

Colony form and septa behaviour are of considerable taxonomic importance in *Tabellaria*, and failure to appreciate this has led to the frequent confusion of three species under the name *T. fenestrata* (Knudson, *Ann. Bot. Lond.*, 1952).

Thirteen characters show quantitative or qualitative variation in *T. flocculosa*, and different combinations of these characters were illustrated by drawings of specimens from (a) a single sample, (b) different parts of the same lake, and (c) the same lake at different times.

Geographical variation was also illustrated by drawings of plankton strains from the English Lake District, where all but two of the radially arranged drainage basins appear to have evolved a morphologically distinct strain.

THE ZOOLOGICAL SOCIETY OF LONDON exhibited a collection of ten amphibians representative of some of the South American Salienta. The families Bufonidae, Leptodactylidae, Hylidae and Ranidae and one member of the Aglossa group, the well-known Surinam Toad, *Pipa pipa*, were on view. The latter was not a full-grown specimen but attention was drawn to the particular breeding adaptation of these toads wherein the young tadpoles pass through all stages of metamorphosis whilst deposited in individual cavities on the back of the female.

As well as *Pipa*, a second entirely aquatic frog was shown, the Demerara Frog, *Pseudis paradoxa*. When fully grown these frogs are only about two and a half inches long, but it is remarkable that the tadpoles may attain twelve or fourteen inches in length before reducing in size prior to metamorphosis.

Two species of Bufonidae were shown, *Bufo marinus* which is one of the giants of this family, and a far smaller, but equally active *Bufo spinulosus*, the Chilean Toad found on both the east and west coasts of South America.

The two largest frogs shown were the South American Bull Frog, *Leptodactylus pentadactylus* and the Ridged Escuerzo, or Horned Toad, *Ceratophrys dorsata*. The latter well displayed the bright but protective coloration, the triangular appendages above the eye, and the enormous mouth so typical of this genus. A juvenile specimen of the Brown Escuerzo, *Ceratophrys americanus*, also exhibited the pronounced burrowing activities of this whole family.

Two species of Arrow Poison Frogs, *Dendrobates auratus* and *D. leucomelas*, demonstrated the remarkably vivid colours typical of this genus, the colours being a warning character, as the smooth skin contains tiny glands which exude a poisonous fluid.

One Brazilian Tree Frog, *Hyla mesophaea*, completed the exhibit as an example of the enormous number of tree frogs found throughout all of South America.

The living terrestrial Arthropoda, exhibited on behalf of the Zoological Society of London by Mr. L. C. Bushby, consisted in the main of Orthoptera. Representing this order were two species of Phasmids, a mature female Ceylon Leaf Insect, *Phyllium pulcrifolium*, and the Javan Stick Insect, *Orxines mackloti*, an adult pair and two immature specimens. Both species are excellent examples of protective mimicry in form and colour. Two species of Mantids were shown, one East African, *Sphodromantis* sp., and one West African, *Polyspilota aeruginosa*, both reared from ootheca sent earlier in the year from Africa.

Of the two families of grasshoppers, the Acridiidae were represented by *Tapesia grisea*, a short-winged species, and *Phymateus morbillosus*, a species somewhat variable in size, and colourful in the immature stages. Both species are distasteful and emit an ill-smelling froth from the thoracic region when disturbed. One example of the Tettigonidae, the Long-Horned Grasshoppers, was shown in the species *Madiga aberrans*, a heavily built wingless insect with a strongly spined thorax.

A nearly mature example of the British Mole Cricket, *Gryllotalpa gryllotalpa*, represented the Gryllidae. In this species the strong, fossorial fore-legs are well displayed and also the insect's ability to move backwards at speed.

Two large spiders were also exhibited, one a large, hairy species, a member of the genus *Eurypelma* from Texas, with orange-red tibia, and the other a member of the genus *Torania*, a type common in tropical Africa and often found in buildings there.

IMPERIAL COLLEGE OF SCIENCE AND TECHNOLOGY. Blood parasitic Protozoa of small wild mammals in Britain. [Shown by Miss B. JACOBS.]

Some of the more important new Protozoan parasites from the blood of small wild mammals were shown in the form of microscope preparations of infected blood and tissues. Two Piroplasms occur in the Common Shrew, *Sorex araneus castaneus*, and the preparations exhibited showed the differences between them in size, morphology of predominant forms and mode of division. In the vertebrate host both species are confined to the blood; the vector is not yet known. Three preparations dealt with a fairly common Haemogregarine infection of the voles, *Microtus agrestis* and *Clethrionomys glareolus*. *Hepatozoon microti* (Coles, 1914) differs from the *Hepatozoon* of *Clethrionomys* only in the main site of schizogony and the two are probably identical. Schizogony phases from the liver and lung were shown for comparison.

ROTHAMSTED EXPERIMENTAL STATION. The biology of wild oats. [Shown by Miss J. M. THURSTON.]

A map showed the distribution of the two species of wild oats, *Avena fatua* and *Avena ludoviciana*, found in the British Isles. Specimens and a graph illustrated differences between species in spikelet abscission, habit of young plant, and seasonal germination of seeds. Selections of both species from different localities showed the variation found in colour and hairiness of husk. Growing seedlings raised from these seed-types and photographs of plants in ear showed the resemblance of the plants to each other and to cultivated oats. Two distinctive selections were illustrated by specimens from several localities; one was *A. fatua* with hairy nodes and the other *A. ludoviciana*, later-flowering than the others. Spikelets of three successive generations of *A. ludoviciana* from Rothamsted farm demonstrated that wild oats normally breed true for seed-type. This contrasted with a type intermediate between wild and cultivated oats, which segregated in the next generation into *A. fatua* and the intermediate parent type. The breaking of dormancy by rupturing the seed-coat was shown by germination of pricked but not of unpricked seeds of *A. fatua* and *A. ludoviciana*. Spikelets with large seedlings from the first seeds, small seedlings or none from the second seeds, and dormant tiny third seeds demonstrated the difference in dormancy between successive seeds in the spikelets of *A. ludoviciana*. Photographs showed that seedlings from seeds of *A. fatua* buried 3 inches deep in soil were more numerous and more vigorous than from 6 inches and that seedlings from 9 inches were very few and weak.

UNIVERSITY OF LONDON, KING'S COLLEGE. Chromatography of plant-growth substances. [Shown by Prof. T. A. BENNET-CLARK, F.R.S. and Mr. N. P. KEFFORD.]

There is some reason to suppose that the hypothesis that growth curvatures of plants are due to a single hormone (auxin or indole-3-acetic acid) may not be a sufficiently complete or even correct explanation.

The development of the chromatography enables us to investigate more completely the nature of growth hormones. The demonstration showed the method of extraction with ether and indicated the principles of chromatography and biological assay of the separated products. With this method it can be shown that in a considerable variety of plants there exist (placed in order of partition coefficient) at least four substances, which we are terming α , indole-3-acetic acid, β and indole-3-acetonitrile. The chemical nature of α and β is unknown.

Dr. C. L. DUDDINGTON and Miss S. M. DIXON. Predacious Fungi.

BRITISH MUSEUM (NATURAL HISTORY).

- (a) Ecdysis in mygalomorph spiders. [Shown by Dr. G. OWEN EVANS.]
- (b) First known example of a terrestrial ostracod. [Shown by Dr. J. P. HARDING.]

ROYAL BOTANIC GARDENS, KEW.

- (a) Tropical species of *Utricularia*. [Shown by Mr. P. TAYLOR.]
- (b) The Flora of Kuweit, Arabia. [Shown by Miss P. LEWIS.]

BRITISH MUSEUM (NATURAL HISTORY). Viviparity in deep-sea brotulid fishes. [Shown by Mr. N. B. MARSHALL.]

THE ROYAL HORTICULTURAL SOCIETY showed three series of original drawings from the Lindley Library. The earliest, a florilegium of 46 paintings by Pieter van Kouwenhoorn, has been ascribed to the first half of the seventeenth century, on the evidence of the water-mark upon the paper and the known fact that Pieter van Kouwenhoorn, a glass-painter, was teacher to Gerard Dou from 1624 to 1626. The flowers are favourites of the Dutch gardeners of the period and are painted in body colour with supreme skill.

The second collection of drawings, by the French artist Pierre Jean François Turpin, comprises twenty-five paintings on vellum, similar in style to many prepared in collaboration with his life-long friend Pierre Antoine Pointeau for important botanical works of the early nineteenth century, including those by Von Humboldt, Bonpland and Kunth. These paintings in miniature are notable for remarkable accuracy and delicacy.

A collection of water-colour drawings by British artists was represented in the third exhibit, a collection of interest, not for any rare skill in execution, as were the others, but because it was an honest attempt to provide illustrations of the British Flora at a low price during a period of considerable depression in the study of botany.

William Baxter, attempting a new British Flora, engaged Isaac Russell, C. Mathews and others who were conveniently living near him in Oxford, where he was Curator of the Botanic Garden. These artists had no previous knowledge of botanical work—Isaac Russell was in fact a glass-painter—and it is to the credit not only of Baxter and his artists but of his daughters and daughter-in-law, who were responsible for colouring all the plates, that this venture succeeded.

Some 500 drawings were made and 600 sets of four hand-coloured engraved prints from them, with accompanying text, were distributed on subscription every month from September 1832 until March 1843. At first both artists' and colourists' work was amateurish, but marked improvement is shown in later issues.

The Flora was well received. Loudon wrote in 1835—" . . . the plates equal in excellence any that have been published, and the letter-press is far superior to that of most British Floras."

As the output of a small team, working in a University town, Baxter's work is compared by A. H. Church (*Journal of Botany*, 1919, **57**, 58-63) to that of sixteenth-century Fuchs and his draughtsmen, who were also non-botanical artists.

RESEARCH STATION, LONG ASHTON (UNIVERSITY OF BRISTOL). Rubbery wood in apple trees. [Shown by Mr. ABBOTT.]

The virus disease of apple trees known as 'Rubbery Wood' was demonstrated by Long Ashton Research Station. Two pieces of shoot of the variety Lord Lambourne, one from a healthy tree and one from an infected tree, were exhibited. Though both pieces were of the same age and diameter, that from the healthy tree was perfectly rigid, while that from the diseased tree was flexible and would be easily bent between the hands.

This flexibility is due to incomplete lignification of certain of the woody elements of the xylem and two microscopic slides of transverse sections of shoots clearly showed the difference in staining reaction between the healthy and diseased specimens. The difference between the spreading habit of a healthy tree and the characteristic drooping habit of an infected tree, resulting from this lack of rigidity, was very apparent from photographs.

Though Rubbery Wood is most widespread in the variety Lord Lambourne, it has been recorded on others, and many varieties have been shown to carry the disease without showing any symptoms and to transmit it to healthy Lord Lambourne when grafted. The fruits from infected trees are quite normal, but the yield is much reduced owing to the stunted growth resulting from severe infection.

SCIENCE MUSEUM. Three-dimensional model of a meteorological depression. [Shown by Mr. D. CHILTON.]

An idealized polar-front depression (schematic model). The model consists essentially of two transparent curved surfaces (perspex) defining the boundaries between the three air-masses involved, which differ in physical characteristics (temperature and humidity). It is based on a depression which was centred over Ireland at 18.00 G.M.T. on 29 January 1946, and which was responsible for widespread rain and snow.

The two surfaces intersect the ground at the Warm Front, Cold Front and Occlusion respectively, and on the model these lines are shown in their conventional colours, viz. red, blue and purple.

The area of precipitation is also conventionally coloured green, and perspex arrows indicate the principal air-streams.

A series of weather charts relates the model to the weather, and shows the course of the depression over a period of 18 hours.

THE USE OF X-RAYS IN VERTEBRATE PALAEOLOGY. [Shown by Dr. K. A. KERMACK.]

The exhibit demonstrated the use of X-rays in the interpretation of the internal structure of vertebrate fossils. For this work, the specimens must be very thoroughly prepared; and, in particular, the matrix must be removed from the cavities of the bones. It is possible to achieve this result by the use of the acetic acid technique described by Rixon (*Museums Journal*, 1949)—supplemented by careful mechanical preparation, where necessary. The specimens then become sufficiently transparent to enable satisfactory radiographs to be obtained with the usual medical X-ray apparatus.

Two mammal-like reptiles from the South African Permian were exhibited, a Gorgonopsid, *Aelurosaurus* sp. (British Museum R 855a) and a Therocephalian allied to *Alopecognathus*. The skulls were X-rayed to show the mode of tooth replacement. The radiographs showed that in *Aelurosaurus* replacement was occurring in the upper and lower incisors, canines and cheek teeth, while in *Alopecognathus* only some of the upper incisors were being replaced. The radiographs of the maxillae of this last specimen showed the remains of the roots of the canine teeth which preceded those now functional.

This method enables internal structures to be studied in fossil material, without the necessity of cutting or in any way damaging it.

The X-ray photographs shown were kindly taken by Mr. P. Venning of the Department of Anatomy, University College, London.

PROCEEDINGS OF THE GENERAL MEETING, 8 January 1953

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 20 November 1952, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Dr. F. W. Andrews, Dr. J. Macqueen Cowan and Dr. Charles Mayer.

Mr. Arthur John Juniper signed the Obligation in the Roll and Charter Book and was admitted a Fellow.

The PRESIDENT reported the deaths of Mr. Reginald Evelyn Child Beale and Dr. Royden Samuel Wale, Fellows of the Society.

The following communication was read and discussed :—

Mr. A. E. HAARER. The behaviour of the chief Jute-Substitute plants.
(Discussed by the President, Dr. G. A. C. Herklotts and Dr. C. R. Metcalfe ;
Mr. Haarer replied.)

The PRESIDENT then adjourned the Meeting to 29 January, at 10.30 a.m.

THE BEHAVIOUR OF THE CHIEF JUTE-SUBSTITUTE PLANTS

By A. E. HAARER.

Ninety per cent of jute fibre is used for sacks and wrappings, in which to carry commodities about the world, so it must be cheap to be of real use for this purpose. Even when prices were low we tried to grow jute, or jute substitutes in several of our countries overseas but failed for several reasons, e.g. the absence of suitable mechanization ; lack of experience, particularly of retting ; and the inherent responses of these crops to varying environments were not understood. Crops often failed to grow with the luxuriance that was

necessary to obtain proper yields, although they had been supplied with all their obvious requirements. It is with regard to these responses that I mainly want to talk.

The populations of India and Pakistan are increasing faster than food supplies are being grown to feed the people, so that it will not be possible to devote much more good land to the production of a commodity such as jute. It may become harder to buy food with the money obtained for jute, hence there may even be a curtailment of the increased acreage under jute today when the demand for cheap fibre in a progressive and more populous world becomes greater. Alternative supplies of either jute itself or of a substitute may have to be found at some future date unless we alter the means we now use for the transport of many commodities. In view of this a British working party toured areas where jute might be grown and they decided on Papua and British Guiana, where trials are now in progress. Elsewhere Brazil has had success in the Amazon Valley. It has been thought that parts of the Sudd region of the Nile might be prepared for jute production in rotation with rice, and surveys have been carried out.

The best jute, *Corchorus capsularis*, has not proved easy to establish in different parts of the world, and one suspects some of the influences which affect its substitutes. The inferior species *Corchorus olitorius* can be established more easily, but even with this species one should proceed with caution and by trial and error. It grows wild in many parts of East-Central Africa, and the Uganda government has recently selected strains from the wild growths that will grow 14 feet tall in Uganda (1).

True jute requires an exceptionally fertile soil with ample moisture and a good rainfall. It also requires high humidity to obtain satisfactory growth and yields; in other words, it grows in areas of the greatest value for tropical food crops. The three recognized substitute fibres Kenaf, Roselle, and Congo Jute can be grown with greater ease, and as for Kenaf, *Hibiscus cannabinus*, it is cosmopolitan in its requirements. It can be grown successfully on most kinds of soil provided there is a warm summery growing season of 4-5 months, during which five inches of rain fall every month, or irrigation is used in lieu, and careful consideration is given to the response of the plant to daylight length.

Hibiscus fibre appears to be less flexible than jute, and is therefore not suitable for the finer counts for which a comparatively small proportion of the world's production of jute is used. American interests have recently proved that it is quite good enough for making sacks; in fact, sacks made from it are stronger than sacks made of jute, and they will last longer (2). When trading interests belie the value of jute-substitute fibres we must not forget that Russia has used Kenaf to make herself entirely independent of imported jute.

Although at first it may seem to have no bearing on the substance of this paper, I must go on to mention the manner in which the United States of America on the one hand, and Britain on the other, have tried to make it possible to produce jute-substitute fibres in quantity in other areas.

The United States have succeeded up to a point, for some 9,000 acres of Kenaf were under cultivation in Cuba in 1952, and the seed crop grown during the previous season for expansion purposes amounted to 1½ million lb. Considerable acreages are also being grown in Florida and El Salvador. To overcome the scarcity and high cost of labour the American government persists in believing that the whole process of cultivating, harvesting and extraction of the fibre must be accomplished by mechanical means from start to finish. This means that the retting process must be eliminated and the bast fibres extracted from green stalk direct.

It is this extraction process which has hitherto been difficult to manage. Harvesting by mechanical means has been overcome, and it was thought at first that sisal decorticating machinery could be adapted for use with Kenaf

No matter what was done the percentage of wastage was too high, and the fibre left with too much tissue and gummy substances adhering to its surface (3). Attempts have been made to evolve and try out other machines, but they have given too small an output, or have created tangling. It has been possible to invent efficient stripping machines to take off the bark in ribbons from the stalk and thus save on the transport of the fibrous material from the field to an extraction centre (4).

The greatest snag of all is presented by the photo-periodic responses of the Kenaf strains the United States of America have used. Their *Hibiscus cannabinus* stock has flowered when the seasonal length of daylight is reduced to about $12\frac{1}{2}$ hours, and this has happened no matter when the seed has been sown (5). The period of longer daylight is used successfully to keep the plant growing, and thus produce a tall growth and a satisfactory yield of fibre by the time flowering begins; or the seed is sown much later so that a stunted growth is given by the time flowering begins to facilitate the harvesting of a seed crop.

The snag is that a large area grown for fibre must all be harvested at once. The yield of good quality fibre is at its maximum when the plants begin to flower. Afterwards the fibre becomes coarser, and the stalk too dry to decorticate (5). Beforehand, the quality may be as good but the yield is progressively less. For best yields, there is a critical period of about a fortnight when harvesting for direct decortication may take place, and it is impossible to stagger the harvest except by cutting early and sacrificing yield.

British research has developed better harvesting machinery and stripping machines which will harvest bark ribbons during the critical period at a faster rate, and these machines have recently been used in a pilot field of jute in British Guiana. We believe that retting must be retained, and that bark ribbons should be dried and stored to give material for all-the-year-round working. On the one hand, the retting process costs a little more, but the American plan necessitates the use of top-heavy mechanization, and the machines must be idle for most of the year unless harvest can be widely staggered.

Both schemes could be greatly facilitated if harvesting could take place over a much longer period, and it would seem that the best chance of arranging this is by making use of the plant's responses to daylight lengths, light intensities and possible seed dormancies.

In early American literature the Roselle is given credit for responding in a remarkable degree to photo-periodicity, but this was later corrected when it was discovered that the material they had imported, and had grown, was not *Hibiscus sabdariffa* at all, but the species *H. cannabinus* (5). Not all our British fibre specialists have noticed this correction, and corrected their own references. The Americans imported seed of *H. cannabinus* from Java of types that had been originally selected by the Howards in India, though something must have happened to the labelling on the way because the so-called *viridis* variety of Cuba cannot possibly be the Howards' *viridis* which was discarded in India (6). It is curious that seed was not taken from India direct, nor was the Type No. 3 used, which the Howards selected as the best, and caused to be distributed throughout India.

However, the Americans have worked on their original importation and have selected a great many numbered strains, many of which give exceptional yields. They all, however, appear to respond to shorter hours of light and flower at $12\frac{1}{2}$ hours daylight. This happens in Cuba towards the end of September and early October. A crop grown from Cuban seed flowers in Southern Rhodesia 20° South in April, when daylight length corresponds to $12\frac{1}{2}$ hours, and reports have been received that it flowered much later than other local strains of *H. cannabinus* (7).

The American authorities have recently imported seed of *H. cannabinus* from all over the world. Seed from Korea and Manchuria, grown among tests

in Cuba for nematode resistance, gave poorer yields because they matured earlier than American strains (8). It has been reported in Formosa and Japan that the response to daylight may vary. Persian material is said to include early maturing varieties, just as the Howards reported from India, their Types 5 and 6 as early, and very early, and their Types 4, 7 and 8 as being late (6).

The whole situation appears to be confused, because, in the absence of appropriate research we cannot be sure whether the earliness in such cases as these can be attributed to an inherent character connected with temperatures, moisture, and end of growing season, or whether there is a varying inheritance in regard to a daylight response. Where the Cuban strain flowered in April in Southern Rhodesia, the end of the rains occurs towards mid-March, and average maximum and minimum temperatures begin to fall about the same time, doubtless assisting maturity.

The wild *Hibiscus cannabinus* plant varies in regard to many characters in Africa, and it appears to be a wide mixture of types. The Howards made selections from only the cultivated types in India, and no-one, as yet, has made an exhaustive examination of the African material, although this was suggested by Pole-Evans as far back as 1917. Seed was collected wholesale in the Transvaal for the South African Government in 1946, but the authorities soon abandoned the use of the wild mixture for two reasons: uneven yield and seed dormancy. Only about 5 per cent of the seed germinated at once and dormancy had to be broken by the use of acid. That there is no problem of dormancy in India helps to prove that Africa is the home of this plant.

Why should dormancy and periodic awakening be found in a species so tied up with seasonal daylight lengths unless the successive germinations respond in a different manner to photo-periodicity? Dormancy is, of course, helpful towards survival, though in the case of this *Hibiscus* it would only appear helpful if the dormant seed awakened at a time when the season ahead permitted a proper period of growth before short daylight occurred, with its influence on flowering. Stunted growths are seldom seen in nature where the plants must compete with tall grasses and vegetation; indeed, the acropetal system of flowering must carry the flowering stem rapidly taller to correspond with the growing season and competing vegetation.

Furthermore, it is interesting to record how the *Hibiscus cannabinus* plant is found growing wild at all latitudes in Africa from Egypt to the Cape. I have seen *Hibiscus cannabinus* growing in many places near the equator in Tanganyika Territory as tall as 8 and 10 feet, where the total hours of daylight of use to growth, rarely exceed $12\frac{1}{2}$ hours, and where Cuban plants would surely grow no more than a foot or two tall, and begin to flower and seed almost at once. One wonders if there is a similar mixture of *H. cannabinus* types throughout Africa, or whether mixtures have evolved, or differ according to latitude. If there is one mixture, then do some of the types favour one latitude, and others another, thus automatically creating a zone? It would be of interest and indeed of great importance to test such a possibility.

The Overseas Food Corporation has been growing considerable areas of *Hibiscus cannabinus* in Tanganyika Territory at a latitude of 7-8° South, where the wet season begins towards the end of November and ends in April. A total day-length of $12\frac{1}{2}$ hours or less begins in March and continues until nearly September, when it increases to nearly 13 hours. The Overseas Food Corporation has tried three strains of seed: one from Egypt; one from Calcutta, India; and one from Cuba. The Egyptian strain flowered in 55 days from germination, the Indian strain 60-65 days, for an average of 3 years, and the Cuban strain within 65-70 days, for an average of 2 years; thus the beginning of harvest time may be staggered by 15 days, which would allow the spread of harvesting over 15 plus 10 days, during the best time for yield

and quality (g). Unfortunately the actual times of sowing, or the actual dates of flowering, have not been given in the information I have had to date, but a growing season of only 55-70 days is not sufficient to give a tall enough growth for good yields of fibre, and the authorities have the idea that the area might be of greater use for the growing and propagating of seed supplies for other regions.

So far none of the local wild varieties of *Hibiscus cannabinus* have been tested there, though it is the intention to try them out this year. If the wet season began to time in November, and seed was sown at once, there should be a period of about 100 days for growth before flowering began about March, and if irrigation were available to start the germination a fortnight earlier it should be possible to produce fibre in this region of Tanganyika, irrespective of the responses of the wild varieties which might be found more fitted to that environment.

Following numerous sowings all the year round, and careful tests in Java, Bolhuis states that *H. cannabinus* shows very little response to daylight length, and a graph is shown in Bulletin No. 44, dated 1940, of the General Agricultural Experiment Station. Now this is extraordinary! How can Kenaf show no response to periodicity in Java, and such a remarkable response in Cuba and elsewhere? The strain, or type experimented with, might be different from those imported by the United States of America from Java, and it might conceivably be similar to the wild strains found in Equatorial Africa, where short daylight does not appear to have a stunting effect. The duration of daylight in Cuba, 20° North, has a little wider variation than that found in Java, 7° South. The minimum length of daylight in Java is approximately 12 hours 17 minutes, and in Cuba 11 hours 50 minutes. The maximum length in Java, is 13 hours 28 minutes, and in Cuba 14 hours 10 minutes. The difference between low and maximum in Java is approximately 1 hour 10 minutes, and in Cuba 2 hours 20 minutes, throughout the year, and, for the purpose of photoperiodicity, the length of civil twilight must be added before sunrise and after sunset. Toxopeus gives the difference in time as only 48 minutes.

One might state here, that a close study of the *Nautical Almanac* in regard to the hours of sunlight plus civil twilight on the equator, shows that total daylight duration varies slowly from two periods of approximately 12 hours 53 minutes about the end of June and the end of December, to low periods of 12 hours 47 minutes at the end of February and the end of August. The actual periods of light influence to plants would be about 15 minutes less than these times. I must also state that I talk of length of daylight as influencing flowering, whereas it may well be in accord with recent research that the length of darkness is the controlling factor. On the equator itself, therefore, the difference in time is only 6 or 7 minutes between longest and shortest day, and it is possible that a race of *H. cannabinus* might be found growing there which is influenced more by moisture and temperature than by photoperiodicity, unless the intensity of sunlight plays its part in making the problem more complex.

A study of waxing and waning daylight hours at the different latitudes then poses a question regarding this African seed dormancy. Are the periodic germinations linked with seasonal moisture and temperature plus a ripening or weathering complex, or are they linked in any way with seasonal light influences? It would be interesting to probe this matter exhaustively, for it seems to me that the best hope of staggering harvesting in any land in future is by the use of these daylight responses.

Neither would it do any harm to study the possible genetic variability of plants arising from delayed germination, a matter that seems to have been neglected in the past in regard to many of our crops which exhibit this phenomenon in the wild state. Unconscious selection for quick germination

may have lost count of characters which might have been inherent in successive germinations, leading, for instance, to the possibility of cold resistance.

Returning to the Roselle, which, after the Americans had corrected their initial mistake, was thought to show nothing like the same response to photo-periodicity as its cousin Kenaf, Bolhuis has recently proved in Holland that this plant is indeed responsive to short daylight. I have myself sown imported seed of the edible Roselle on an experiment station in Tanganyika, and found the plants grew stunted and flowered at less than 2 feet tall in spite of a fertile soil and ample moisture. The sowing took place mid-February as the rains began at 7° South, when the total daylight length was about $12\frac{3}{4}$ hours, falling to $12\frac{1}{2}$ within less than one month from sowing.

The latitude in Java is about the same, and the Dutch discovered that the Roselle had to be sown for fibre purposes at a favourable season of the year. If it were sown after the middle of October the crop did not give economic yields. The Roselle takes longer to mature, and requires 6 months' growth to give the desired length of stalk. The variety concerned in Java is the *altissima* inedible type, and when it is sown in mid-October it has slightly more than 13 hours daily daylight, rising to about $13\frac{1}{4}$ hours in November–December, and falling to about $12\frac{1}{2}$ hours soon after the beginning of March, giving barely sufficient time for proper growth. For fibre purposes the crop is usually sown in August/September towards the end of the short-day season, thus the seedlings have appeared above ground by the time the longer days begin. For seed purposes the crop is best sown in January and February, so that it has only three months, or half the period of growth, before flowering begins on stunted plants about April.

Bolhuis states that considerable sums of money were lost before this discovery, when large-scale plantings were sown at other times of the year, under the mistaken impression that irrigation would permit the cultivation of the plant all the year round. For purposes of record it might be stated that Bolhuis has informed me that Dr. P. J. S. Cramer introduced different strains of the Roselle to Java from Hawaii, including the *altissima* variety (10).

At Wageningen in Holland experiments have recently been made in cultivating the Roselle. Grown under temperate conditions, and sown at a normal time, the plants started flowering in September–October, and this generally resulted in a few unripe seed capsules which did not mature owing to low temperatures. Sown in February under glass the plants flowered when only 10 inches tall. After a little less than a month, growth started again, and while the set capsules matured, all the very young fruits and the last flowers dropped.

When large plants in a summer hothouse were temporarily exposed to short-day conditions, flowering began after about 10 days, and fruits were set. Re-exposed to long days the fruits, flower buds and flowers dropped within a few days, and growth was resumed.

Toxopeus at Buitenzorg interested himself in the influence of daylight on the Roselle for the purpose of breeding, because by deliberately manipulating daylight length he could shorten the time needed to raise four inbreeding generations. As an interesting side-issue he speaks of the existence of hereditary differences in the Roselle's reaction to photo-periodicity. He records that samples of seeds received from the Gold Coast reacted quite differently, for some plants flowered in September and others flowered profusely in December at a time of the year when Javan varieties refused to flower. In Java flowering normally starts abruptly at the beginning of April and ceases gradually during October. He concludes that varieties exist, to use his own words, "with a shorter as well as a longer flowering period than the fibre-varieties cultivated in Java". He states, again using his own words,

"a mechanism that is highly sensitive indeed and reacts on differences in daylength of some minutes, is demonstrated here".

But he was interested only in plant breeding and was not thinking of staggering harvest. It seems, therefore, to me, that the chances of staggering harvest by making use of the varying reactions to daylight length, both for Kenaf and the Roselle, are very good indeed.

Lastly we come to Congo Jute, *Urena lobata*, a more distant cousin to the *Hibiscus* genus, and one that has spread itself throughout the tropics and sub-tropics of the world, probably from Asia. Very little fundamental research appears to have been carried out, and there is nothing to prove or disprove a theory that there may be, or may not be, a photo-periodic response, at least in some of the types. It has spread by itself through many latitudes north and south of the equator, and whether there has been a natural selection of types, or not, is at present unknown. The plant varies a great deal in form.

In the Belgian Congo early and late maturing types have been found. De Groof records that provided there is moisture and warmth, the plant can be grown successfully for fibre all the year round. This is not conclusive, however, unless the height to which the plant grows is compared season by season, and the dates of flowering, and the separate yields are all recorded. De Groof makes a great point about delayed growth in the seedling stage, and of how weeds may overgrow the seedlings because of this reason. During a test in Cuba it was seen that germination was so patchy in the beginning that it was thought the sowing had failed, in spite of the great care with which sowing had been carried out on prepared land. A week or two later successive germinations took place and the bare patches closed in. The plants that were delayed apparently grew fast enough to catch up with the others, but nothing else was recorded except the remark that a number of seeds which germinated later still, grew plants that shrivelled and died because they were overshadowed (12).

The seeds of *Urena lobata* both in the Congo and in Cuba had been sown in their separate carpels, and the permeability of these additional envelopes and the fact that the seed itself was not necessarily in contact with the soil may have caused variable but short delays in germination.

If, therefore, pilot schemes are begun in future in advance of big-scale plantings of these jute substitutes, they should be associated with research to clear up the points which I have enumerated. In the meanwhile, and before such knowledge has been gained, in the event of any sudden requirement for a large production of these fibres, it would be wise to obtain and sow seed of strains that have been successful and have given known responses at similar latitudes.

Moreover, in regard to the two *Hibiscus* species, a study of the *Nautical Almanac*, and of the hours of daylight plus civilian twilight at different latitudes north and south, will give a helpful indication of when these crops should be sown, and when they should be ready for harvest. If the temperatures are sufficiently warm, the soil of sufficient fertility, and the period of longer hours sufficiently long, the absence of rainfall either at the beginning or end of the growing period could be overcome, perhaps, by irrigation. Lastly, on account of the potential strategic importance of *Hibiscus cannabinus*, and the desirability of staggering harvest at the time of best yield, I feel that investigations concerning the variation in the plant's response to daylight, and also possibly its seed dormancies, should not be delayed.

During the last few years a number of pioneering attempts have been made to grow jute substitutes, not always with success, and if this paper helps to stop the irresponsible movement of seed strains from latitude to latitude without careful consideration of the points raised, it should serve a useful purpose.

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**PROCEEDINGS OF THE RESUMED MEETING,
29 January 1953**

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President,
and later Dr. W. E. SWINTON, Vice-President, in the Chair.

The PRESIDENT reported the death of Professor Frederick Ernest Weiss, F.R.S., Fellow of the Society, and moved the following Resolution, which was passed in silence, all present standing in their places :—

The Fellows of The Linnean Society of London having heard with the deepest sorrow of the death of Professor Frederick Ernest WEISS, F.R.S., desire to place on record their high appreciation of the services he has rendered to the Society during his sixty-five years of Fellowship. Elected in 1888, he served on the Council from 1907-09, 1923-25, 1931-35 and 1937-40. He was appointed Vice-President 1924-25 and 1934-35, and held the office of President from 1931-34. Professor Weiss was awarded the Linnean Medal in 1949. During his long Fellowship of the Society he showed the greatest interest in all its activities, being frequently present at its Meetings and a regular reader in the Library, to which he gave many gifts.

Deploing the loss of so distinguished a Fellow and true friend of the Linnean Society, the Fellows desire to express their deepest sympathy with Mrs. Weiss and her family in their bereavement.

A DISCUSSION on the PROBLEMS OF DISTRIBUTION OF ANIMALS AND PLANTS IN AFRICA was opened by the President, Mr. E. Milne Redhead, Mr. R. E. Moreau, Dr. A. Tindell Hopwood, Mr. P. F. Mattingly, Professor P. C. C. Garnham, Dr. W. E. Kershaw and Dr. E. B. Worthington.

The following took part in the Discussion :—

The PRESIDENT, Dr. C. A. Hoare, Dr. F. R. Irvine, Mr. E. Schelpe, Mr. A. W. Exell, Mr. G. Fryer, Professor E. P. Stebbing, Mr. C. H. N. Jackson, Mr. R. W. J. Keay, Dr. A. J. Cain and Dr. E. Trewavas; Professor Garnham, Dr. Kershaw, Mr. Milne Redhead, Mr. Mattingly, Mr. Moreau, Dr. Worthington and Dr. Tindell Hopwood replied.

The following papers were read in title :—

‘Critical Observations upon Siwalik Deer.’ By AUGUSTO AZZAROLI.
(Communicated by Dr. A. Tindell Hopwood, Sec.L.S.)

‘The External Gills of *Gegenophis* Embryos.’ By L. S. RAMASWAMI.
(Communicated by Dr. H. W. Parker, F.L.S.)

DISTRIBUTIONAL RANGES OF FLOWERING PLANTS IN TROPICAL AFRICA

By E. MILNE-REDHEAD.

(With 16 text-figures.)

I shall confine my remarks to the distributional ranges occurring in the flowering plants of the tropical region of Africa and not try to demonstrate the many connections which occur between the flora of tropical Africa and that of other continents and countries, although such connections will inevitably show themselves. In attempting to demonstrate some of the more common patterns of distribution which occur within the continent, and that are repeated again and again in quite unrelated plants, I can but show a few of their variants; you will, I know, think of others.

All the examples are taken from groups on which I have done some work, or of which the taxonomy has recently been revised. Water plants, coastal plants or species of very specialized habitat have been avoided.

To understand the distribution of flowering-plants in tropical Africa, one should have a general idea of the vegetation and the chief factors that affect it, namely, the rainfall (the total and how it is distributed) and the altitude. Other factors, which play a most important part, are fire, man, grazing animals and the incidence of frost. You are all familiar with the topography, and the effects on the vegetation of fire, man, animals and frost need not be enlarged upon.

The distribution of rainfall is summarized on a map (fig. 1). Owing to the small scale, certain small areas of heavy rainfall are not shown. For instance, rainfall in excess of 60 inches (c. 1,500 mm.) per annum occurs on the Usambara, Nguru and Uluguru Mountains, and on the islands of Zanzibar, Pemba and Mafia. In general, the areas with a rainfall of less than 60 inches are subject to one or more long rainless periods each year. The area of low rainfall on the coast of the Gold Coast near Accra should be noted.

Fig. 2 is a vegetation map again summarized on very broad lines. For convenience I have followed the terminology used by R. E. Moreau in his excellent paper on “Africa since the Mesozoic”. On this map, the crosses show mountains and highlands where montane forest may occur.

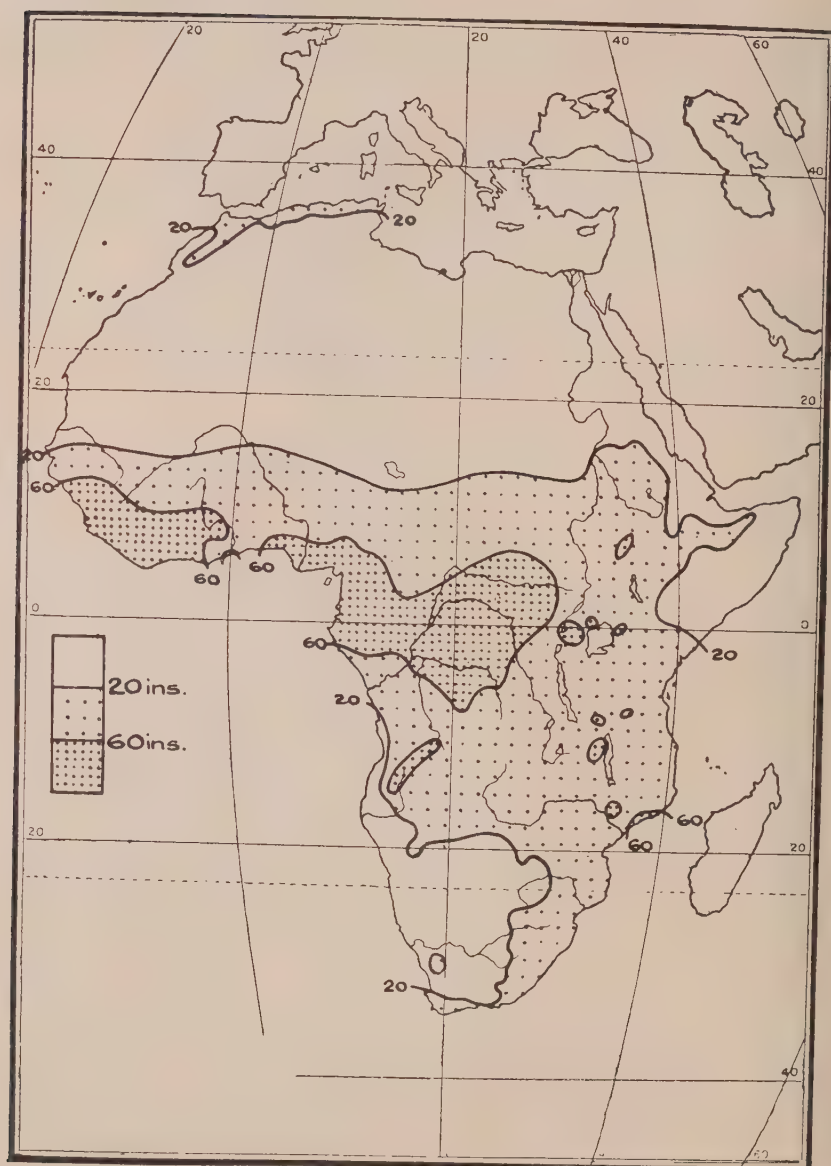


FIG. 1.

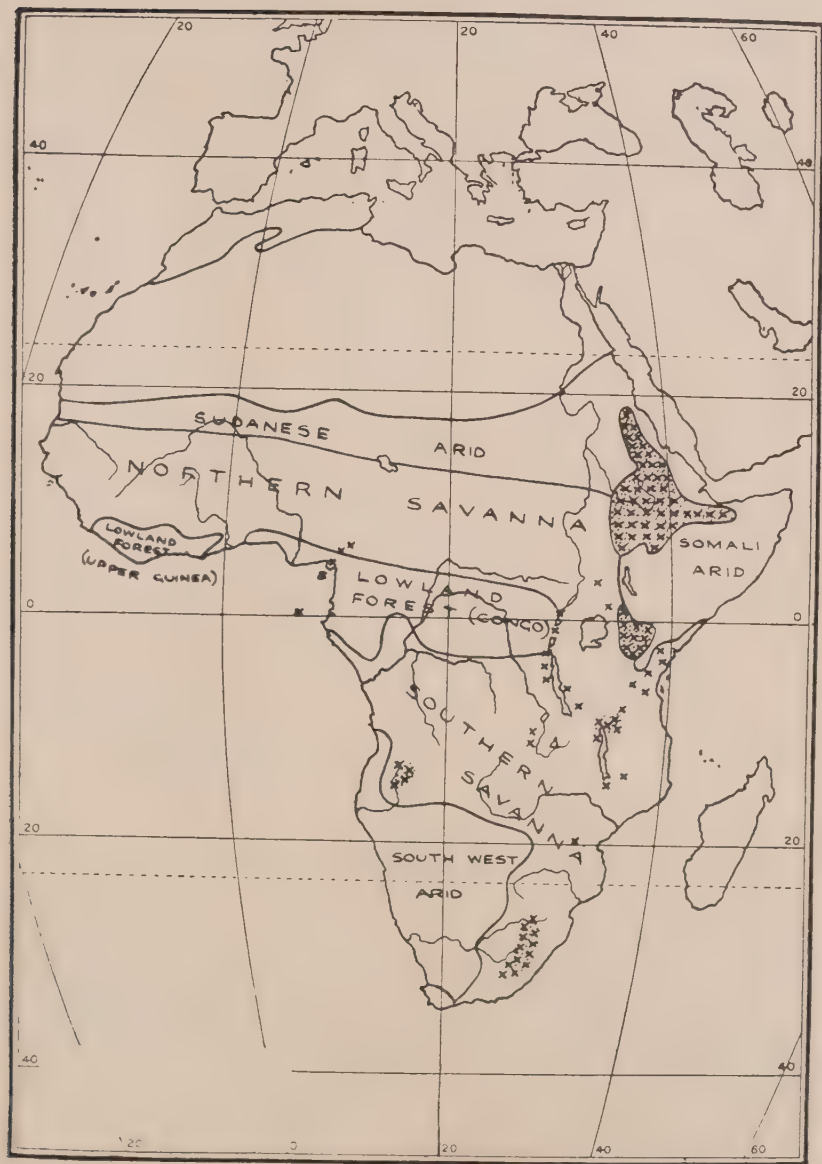


FIG. 2.

I would emphasize the three arid regions, of which the Sudanese Arid is by far the poorest in genera and species of flowering plants. Several characteristic plants of this division extend eastwards across Arabia to Persia and Baluchistan. The Somali Arid also occurs in S.W. Arabia. Of these three, the South-West Arid is floristically the richest.

Then there are two savannah regions, the Northern and the Southern, of which the latter is considerably the richer floristically. Both these regions may be subdivided in general into a wetter and a drier zone. In the Northern Savannah the drier northern (Sudan) zone is characterized by the presence of numerous *Acacia* species whereas the southern (Guinea) zone has a climax vegetation (seldom reached) consisting of broad-leaved deciduous woodland. *Isobерlinia* commonly occurs in this zone, but *Brachystegia*, so abundant in the corresponding zone of the Southern Savannah, is absent. Similar subdivisions may be recognized in the Southern Savannah, with the addition of a thicket vegetation in the dry areas of central Tanganyika, which are infested with tsetse fly.

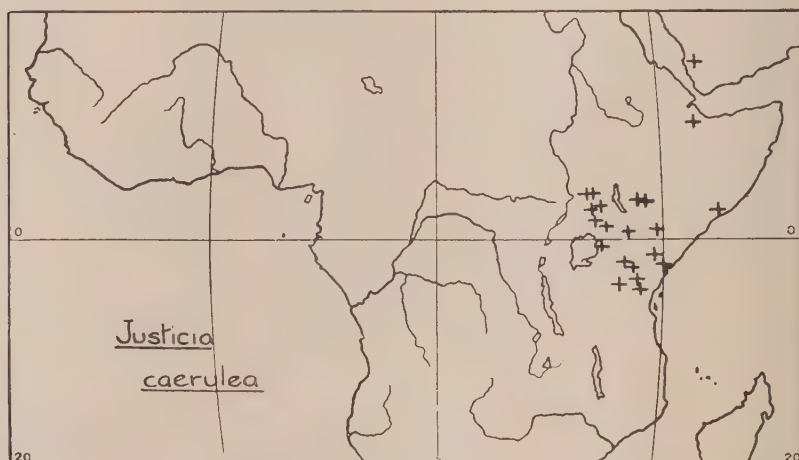


FIG. 3.

Thirdly, there is the evergreen rain-forest. In addition to the main areas of forest shown on the map, there are small relict areas of lowland forest along the east coast which are different floristically from the Congo and Guinea forests. Kakamega Forest in Kenya may be considered the eastern limit of the Congo forest, which at one time was much more plentiful in Uganda than it is today. The gap in the forest along the west coast corresponds with the area of low rainfall already mentioned. The constriction in the Congo forest is of interest, as here there may have been a route for the migration of savannah species from north to south or *vice versa*. Forest extends into the savannah in the form of fringing forests along the rivers.

Upland (montane) forests are scattered throughout eastern Africa where suitable elevation and rainfall exist: they also occur locally in Angola, the Cameroons and on the islands in the Gulf of Guinea.

Of the characteristic plants of the Sudan and South-West Arid divisions there is nothing in particular to say. The distribution of *Justicia caerulea* Forsk. (fig. 3) is typical of a plant occupying the Somali Arid division. The small number of records from Somaliland is probably due to a lack of collections from there. The same plant occurs in Karamoja, in the drier parts

of Kenya and the dry region of Tanganyika around Kilimanjaro and the Pare Hills. It is not particular as to altitude and is found from about sea-level to nearly 6,000 ft. (1,800 m.) in Arabia. Above that altitude conditions might be too cold for it. It requires a 30 inch (750 mm.) annual rainfall or less and long dry seasons. Many other Somali plants show this pattern, but often their range is more restricted and local.

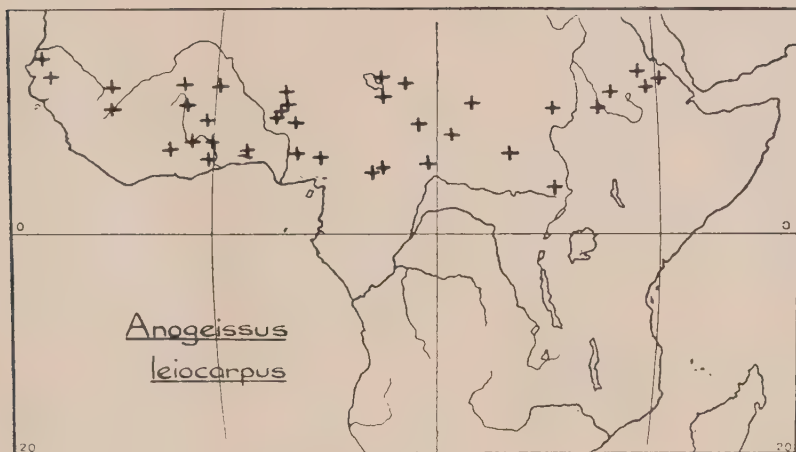


FIG. 4.



FIG. 5.

Anogeissus leiocarpus Guill. & Perr. (fig. 4) shows a typical Northern Savannah distribution. Other species may be more restricted in their distribution, being confined to the eastern or the western end of this belt, or may occur quite locally within it. This interesting Combretaceous tree is unknown in the Southern Savannah. *Clematis welwitschii* Kuntze (fig. 5) is its counterpart in the south. A third savannah plant is *Amorphophallus abyssinicus* (A. Rich.) N. E. Br. (fig. 6), a species which occurs both in the Northern and Southern Savannahs. Here we have an excellent example of the importance of getting the taxonomy of a group right before studying its distribution. Until recently the specimens here plotted had been placed in six different species on account of the use (in my opinion) of wrong diagnostic characters. It was called *warneckii* in the Gold Coast and Togoland, *barteri* in Nigeria, *chevalieri* in Ubangi-Shari, *schweinfurthii* in the Anglo-Egyptian Sudan, *seretii* in the Belgian Congo and *mossambicensis* at the southern end

of its range. Its correct epithet, *abyssinicus*, was not in current use! One of the shrubs so characteristic of the thickets of central Tanganyika is *Anisotes bracteatus* Milne-Redh. (fig. 7). It and many other unrelated species are endemic in these thickets. Before leaving the savannah, I must mention the endemism which occurs in the small dry coastal region of the Gold Coast and Togoland. It would be interesting to know if a similar endemism occurs in the fauna of these two thicket areas.

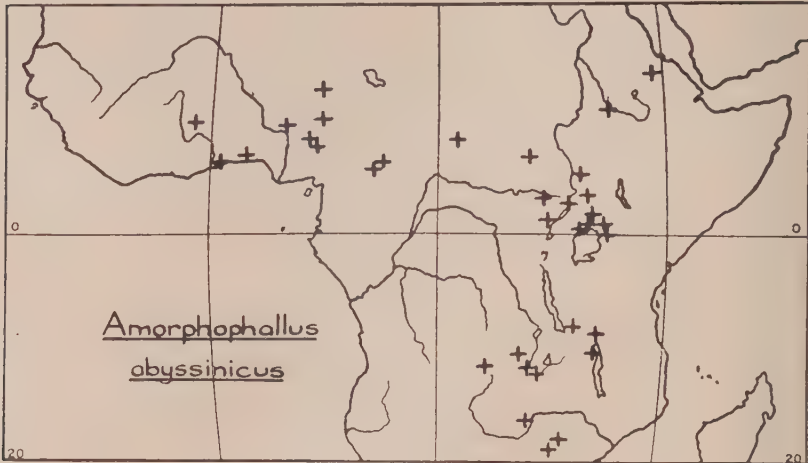


FIG. 6.

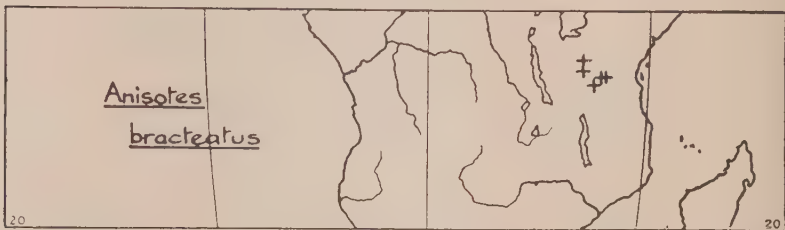


FIG. 7.

Harungana madagascariensis Poir. (fig. 8) is a characteristic second growth tree of rain-forest that also occurs in suitable fringing forest provided the annual rainfall is not less than about 50 inches (1,200 m.). It is a lowland forest species. In Tanganyika it occurs wherever the annual rainfall is over 60 inches and the altitude is less than 6,000 ft., and its range extends to the eastern coastal forests, to the islands just off that coast, as well as to Madagascar and Mauritius. Note that the rainfall, rather than the topography, influences it: it crosses the Congo-Zambesi watershed and occurs along the upper waters of the Zambesi basin.

More restricted forest distributions are shown by *Marantochloa cuspidata* (Roscoe) Milne-Redh.* (fig. 9) which is not known to occur east of the dry gap in the Gold Coast, and *Erismadelphus exsul* Mildbr. (fig. 10) from the rich forests of Cameroons, Gaboon and the Belgian Congo, reaching its western

* *Marantochloa cuspidata* (Roscoe) Milne-Redh., comb. nov. *Maranta cuspidata* Roscoe, Scitam. t. 31 (1828).

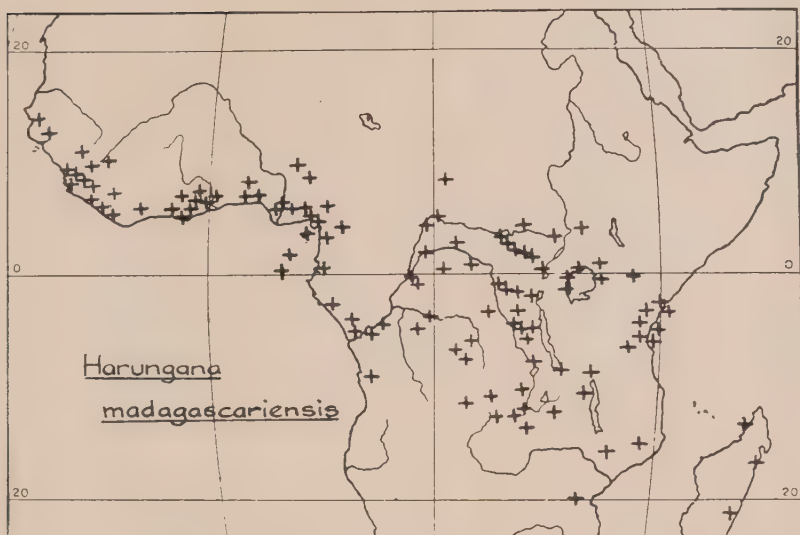


FIG. 8.

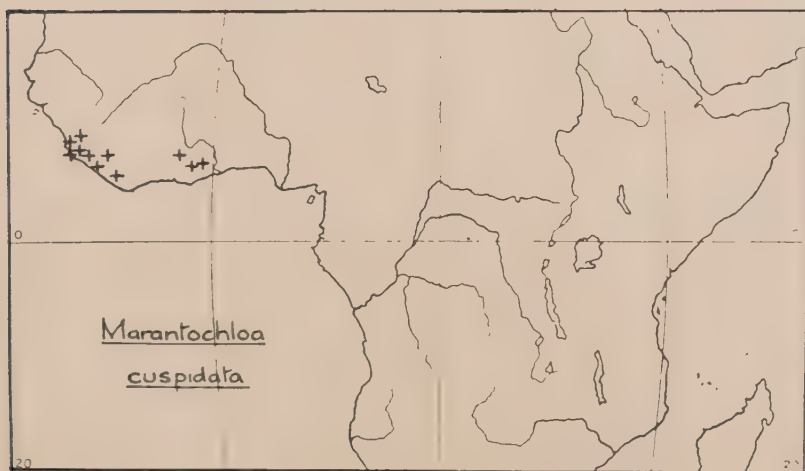


FIG. 9.

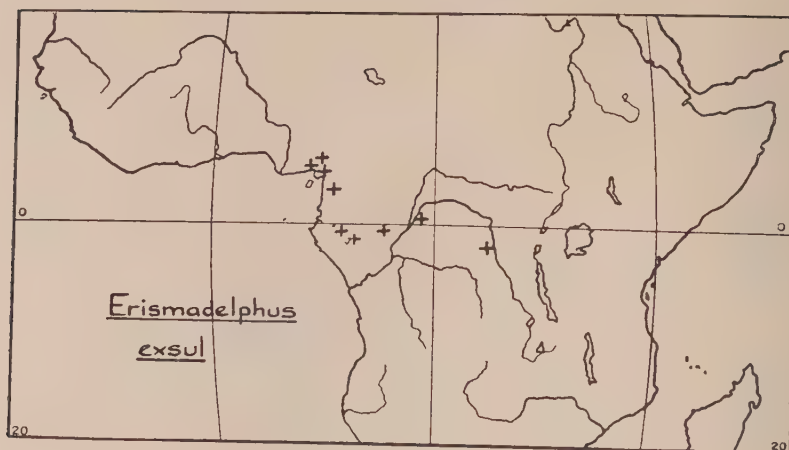


FIG. 10.

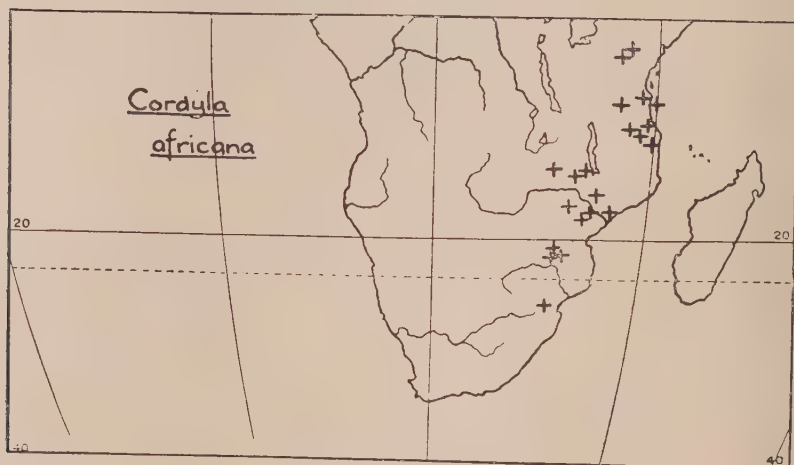


FIG. 11.

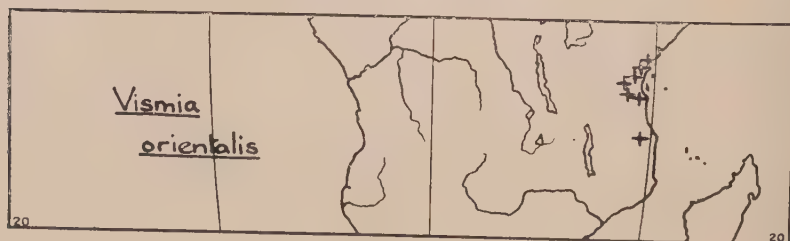


FIG. 12.

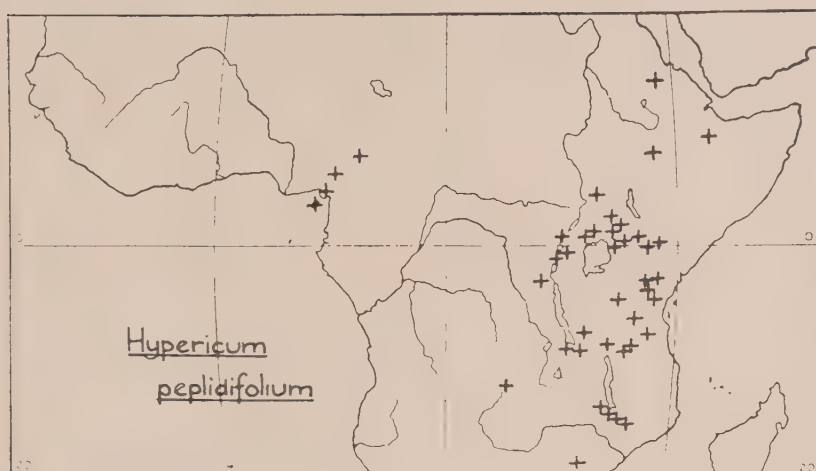


FIG. 13.



FIG. 14.

limit in the forests around Calabar in Nigeria. *Cordyla africana* Lour. (fig. 11) is a tree of the eastern forests, which also gets inland in fringing forests, but does not reach the Congo basin or the forests around Lake Victoria. *Vismia orientalis* Engl. (fig. 12) displays a still more restricted distribution of the same pattern.

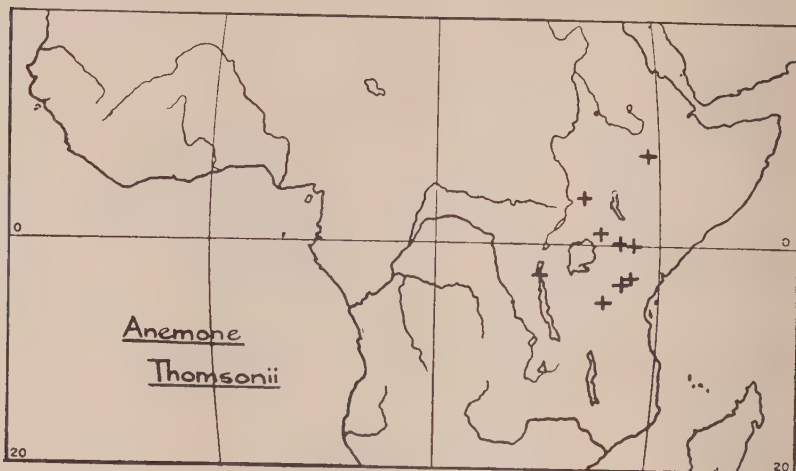


FIG. 15.

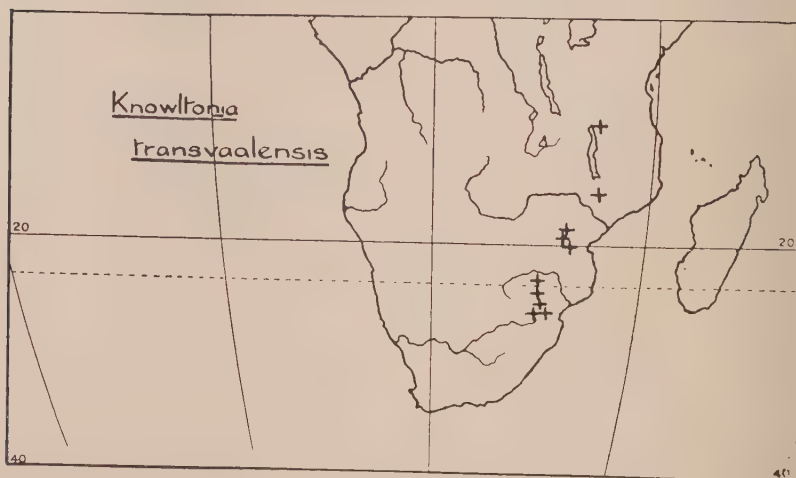


FIG. 16.

Hypericum peplidifolium A. Rich. (fig. 13) is a highland species of grasslands, combining somewhat the montane and the savannah habitat. It occurs on all high ground in East Africa which is not too dry. Note its absence from the centre of Tanganyika, apart from a single occurrence on Mt. Hanang: note also the strong East African connection of the Cameroons and Fernando Po. *Thalictrum rhynchocarpum* Dill. & A. Rich. (fig. 14) is a plant of the edges of montane forests which shows well how widely such plants may be distributed. Here again the same connection occurs with West Africa. *Anemone thomsonii* Oliv. (fig. 15) is a high mountain plant with a restricted

northern distribution on the East African mountains; it is absent from Ruwenzori and the Virunga Mountains, possibly because of the lack of suitable habitat in these much wetter areas. Complementary to *Anemone thomsonii* is *Knowltonia transvaalensis* Szyszyl. (possibly better known as *Anemone whyteiana* Bak. G.) (fig. 16) which is restricted to the mountains from southern Tanganyika to the Transvaal.

I hope that these examples have made it clear that although the range of some species is spread throughout country supporting suitable vegetation, the range of others is restricted within it in varying degrees; but there are, of course, many exceptions to this general rule.

May I end my remarks by appealing to zoologists to refrain from the use of the adjective 'Ethiopian' in the sense of 'tropical African'? At one time, botanists, too, used 'Ethiopian' in this wide sense (cf. *Hypericum aethiopicum* Thunb., a Cape plant described in 1800; *Pilostyles aethiopica* Welw., an Angolan species described in 1869) but of recent years it has generally been restricted to plants characteristic of Ethiopia (i.e. Abyssinia). If this Meeting is an indication that botanists and zoologists are at last prepared to come together to discuss their problems of distribution, it is important that there should be agreement on the use of such a vital and ambiguous term as this.

THE DISTRIBUTION OF AFRICAN EVERGREEN-FOREST BIRDS

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(With 2 text-figures.)

INTRODUCTION.

It might be thought that creatures so highly mobile as birds were less fitted than most to be the subject of zoo-geographical discussion. This, however, is not so. Tropical African birds confine themselves so strictly to their habitats that they are seen outside them very rarely indeed; and where their habitats form ecological islands (as in the case of montane forest birds) the high degree to which some of them show subspecific differentiation is evidence of how thoroughly the populations are reproductively isolated, even when geographically close together. A particularly striking instance will be given below, which shows that isolation of this type can be as effective on the surface of an ancient continent as in a marine archipelago, and to a degree that has probably not been recognized in any other class of organism.

As discussed elsewhere (Moreau, 1952 b), the Ethiopian avifauna (i.e. that south of the Sahara) falls into four main divisions, those of the semi-arid thornbush, the 'savanna', the lowland evergreen forest and the montane evergreen forest respectively. In order to keep the present discussion within manageable limits, it will be concentrated on the two forest avifaunas.

I am indebted to Dr. D. Lack and Mr. D. W. Snow for reading the draft of this paper critically and making valuable suggestions.

THE DISTRIBUTION OF FOREST AND OF FOREST BIRDS.

Following Chapin (1932), it may be accepted that throughout most of tropical Africa the 5,000-foot contour approximately forms the lower limit of the montane birds; but this is subject to significant variation. In particular, where the climate is cooler than the altitude would lead one to expect, the

Montane Forest occurs, at least vestigially, on most of the mountains above 5,000 ft. in tropical Africa (where the timber-line is at about 11,000 ft.). The only extensive areas of montane forest, or of groups of forest patches having high-level connection between them, are those in Abyssinia and the Kenya Highlands. There is no montane forest anywhere in West Africa except on Cameroon Mt. and on the detached mountains of Kupé, Manenguba and Bansa-Bamenda, just to the north (see map in Serle, 1950).

The great majority of the montane forests of tropical Africa are small, occurring on isolated peaks or ridges surrounded by savanna or thornbush. In Nyasaland, forests as small as 200 acres, persisting on island mountains, maintain a typical montane-forest bird-community of up to 24 species (Benson, 1948).

It is worth while to emphasize that under the present conditions, combining a dry climatic cycle with human exploitation on an unprecedented scale, the forests of both types are subject to constant attrition, and it may be doubted whether the distribution of the montane forest in particular has ever been much more discontinuous than it is at present. But at the same time many of the montane forests are surrounded by such exceedingly dry lowlands that, even in the absence of human destructiveness, a general climate far wetter than the present would be necessary for lowland forest to exist there in contact with the montane. At present an actual transition from lowland to montane forest can be studied in unbroken series only in some localities on the eastern edge of the Congo Basin and on a relatively small scale, and with the handicap of exceedingly steep slopes, on hills near the Indian Ocean.

I was fortunate in living for a number of years in one of the last-mentioned localities, in Usambara. There, on the seaward face of the eastern plateau, with a well-distributed rainfall of about 80 inches a year, the original vegetation has survived 'development' enough to provide an example of continuous forest from 500 ft. to 4,000 ft. a.s.l., and elsewhere in the Usambaras up to over 7,000 ft. Seeing that there is no interruption in the tall evergreen forest that clothes the very steep slopes, the change in avifauna that takes place between about 2,000 ft. and the plateau at 3,000 ft. is very remarkable. Confining discussion to the passerine birds, the number of species in the lowland forest is 29; on the plateau there are 42 species, 23 of which do not occur in the lowland (Moreau, 1933 and unpublished). So striking a difference in a space of two or three miles, with only specific, not physiognomic, change in the vegetation, is probably unsurpassed, at any rate in Africa. It may be added that at higher altitudes still, above 4,500 ft., the Usambara forest holds 35 passerine species, 26 of which occur down to 3,000 ft., but only 6 of them below 2,000 ft.

The lowland and montane evergreen forests of course resemble each other far more closely ecologically than either of them resembles savanna, which is so much drier and hotter and is subject to great seasonal changes. It is therefore not surprising to find that the specific composition of the savanna avifauna is almost completely different from that of the forest. What is astonishing is that the difference between the lowland-forest and the montane-forest avifaunas is nearly as great. This is illustrated by the statistics in Table I, which is compiled from Sclater's (1930) classification of the Ethiopian passerine birds. Taxonomic uncertainties being what they are, especially at the generic level, it would be wrong to insist on the exact figure; but it is undoubtedly true that well under one-tenth of the lowland-forest birds regularly occur in any of the montane forests. As regards the genera, only about half those in montane forest are represented also in the lowland. Most of the others are confined to the montane; but they are small genera, and

while some are unquestionably 'good', others are not well thought of by taxonomic 'lumpers'.

It must be emphasized that while there is of course considerable variation in the specific composition of the avifauna of different montane forests, in every such forest, however isolated, all or nearly all the birds belong to typically montane species and genera. A very few cases can be cited in which the montane species that would be expected in a certain niche is absent from a particular montane forest and a 'foreign' species takes its place. (For example, in the Mbulu highlands of northern Tanganyika Territory neither of the 'expected' forest woodpeckers *Mesopicos* or *Campethera* is present and the savanna *Yungipicus* 'deputizes'—Moreau, 1948.) Such exceptional cases confirm the general impression that the montane-forest birds tend to form closely integrated communities which have evolved together (and with the vegetation) for so long that the available ecological niches are thoroughly filled. This view receives further confirmation from the rarity with which a lowland-forest species is found in the montane forest, either as an individual straggler or (with or without subspecific differentiation) as a specific member of a montane community. (The converse is, of course, equally true.) It is in this connection relevant to note that hardly any Palearctic migrants, seventy passerine species of which winter south of the Sahara, penetrate or occupy for the winter either the lowland or the montane forests (Moreau, 1952 a).

TABLE I.—The affinities of the forest avifaunas.

Evergreen forest avifauna	Total number	Number shared with		
		Savanna	Montane forest	Lowland forest
Lowland genera	84	36	29	—
species	216	Nil	14	—
Montane genera	54	27	—	29
species	116	Nil	—	14

For the present purpose, discussion of the geographical distribution of the lowland-forest species can be limited to two points:—

- (1) The comparatively depauperate East African coastal communities differ greatly from the western, about 600 miles distant in the interior at their nearest point, north-east of Lake Victoria; for, while they belong to the same genera, only 18 out of the 50 eastern and south-eastern passerine species also occur in the west.
- (2) There are also considerable differences, but of a rather different nature, between the lowland-forest birds from Cameroons eastwards (commonly known as those of Lower Guinea) and those from the Gold Coast westwards (those of Upper Guinea) on the other side of the savanna gap. There are only about 75 species in Upper Guinea compared with over 150 in Lower Guinea as a whole, and of the 75 only 15 are confined to Upper Guinea.

The montane-forest avifauna demands fuller treatment. Although confined to ecological islands, a large proportion of the montane species are widespread within the inner tropics, but remarkably few of them extend north of 4° N. or south of 17° S. For example:—

- (1) Of 33 species of birds in the montane forests near Blantyre, South Nyasaland, at ca. 15° S. (Benson, 1948), 29 (and all the genera) occur in

Usambara, 700 miles to the north (Moreau, 1933). Again, 140 miles east of Blantyre, on the isolated Namuli Mt. in Portuguese East Africa, there are 25 species of montane-forest birds (Vincent, 1934), 23 of which occur also in Usambara. It is true that there are between Usambara and these southern localities a number of isolated highlands, as suggested even in the inadequate map in fig. 1; but the gaps are thoroughly unsuitable for montane birds, which are never found in them.

- (2) Cameroon Mt. (and its smaller outliers to the north) are separated by 1,300 miles from the next montane forests to the east, Ruwenzori and the Kivu Mts. in Central Africa. The intervening country is not of course dry; the lowland evergreen forest of the Congo Basin covers it and there are no important stretches of savanna, let alone of thornbush. At the same time, there are no intermediate montane 'stepping-stones' whatever, and even along the northern rim (much of it very dry) of the Congo Basin there is hardly any locality that attains more than half the height necessary for classification as 'montane'. Yet of 41 birds species in the montane forest of Cameroon Mt. that do not occur in lowland forest (Serle, 1950; Rand, 1952), 20 inhabit also mountains east of the Congo Basin; and of these 20, 4 are subspecifically inseparable on the two sides of the 1,300-mile gap and 10 extend down eastern Africa as far as Nyasaland.
- (3) Of the total of 116 montane-forest species in Africa, only 16 occur south of the Zambesi (which, at 18° S., is well within the tropics). It is true that the total area of montane forest in Rhodesia and South Africa is small, but there are areas, especially in the Melsetter District, which are at least comparable with the exiguous Nyasaland hill-forests already referred to as maintaining over 20 species of passerine birds.
- (4) The Abyssinian highlands contain some of the biggest montane forests in Africa (cf. Logan, 1948) and are floristically and in other respects a good deal like those of the East African highlands. The southernmost Abyssinian forests are separated from those of the Kenya Highlands by about 300 miles, much of it very dry country at about 2,000 ft., on the east side of Lake Rudolf, and the westernmost Abyssinian forests are separated by about 200 miles of even lower country, also with rainfall under 25 inches a year (Hurst, 1952), from the nearest point in the Imatongs group of montane forests on the Sudan-Uganda border. Although they are so varied and extensive, the Abyssinian forests are remarkably poor in montane-forest passerine birds: they have only 16 species compared with 41 in the Kenya Highlands, 23 in the Imatongs, which are themselves remote outliers of the Kenya Highlands, and 35 in the small area of Usambara. The Abyssinian list is actually smaller than that for some of the Nyasaland forests of a few hundred acres, already referred to. Some important genera are unrepresented, particularly *Apalis*. Moreover, the bulbul family (Pycnonotidae), of which four species occur in the Kenya montane forests, is represented in Abyssinia only by a savanna species.

While these major facts of distribution at the specific level are borne in mind, it is useful also to recall the degree to which subspecific differentiation has taken place between populations inhabiting mountain forests that are often within easy sight of one another. The most remarkable example is afforded by *Zosterops*, which is represented by 10 forms, all allopatric, on their separate mountain masses, in the comparatively small area comprised in Kenya Colony and extreme north-eastern Tanganyika Territory. Possibly they should be grouped in more than one species, though past attempts to do

this are not satisfactory. Their distribution is indicated on the map (fig. 2). Attention is particularly drawn to the line Usambara-Kilimanjaro, on which *stierlingi* is separated by only a dozen miles of thornbush (at 1,500 ft. a.s.l.) from *winifredae*, this by 20 miles of dry country at 3,000 ft. from *mbuluensis*, and this by 20 miles at about 2,000 ft., partly still under ground-water forest, from *eurycricotus* of Kilimanjaro. Only 50 miles to the north of this line are *silvanus* in the Teita Hills and *chyuluensis* in the Chyulus, both islanded in very dry low-altitude thornbush. Again, *kikuyuensis* and *jacksoni* in the Kenya Highlands to the east and west respectively of the Rift Valley, are separated about Naivasha by less than 10 miles of dry country at about 6,000 ft. a.s.l.

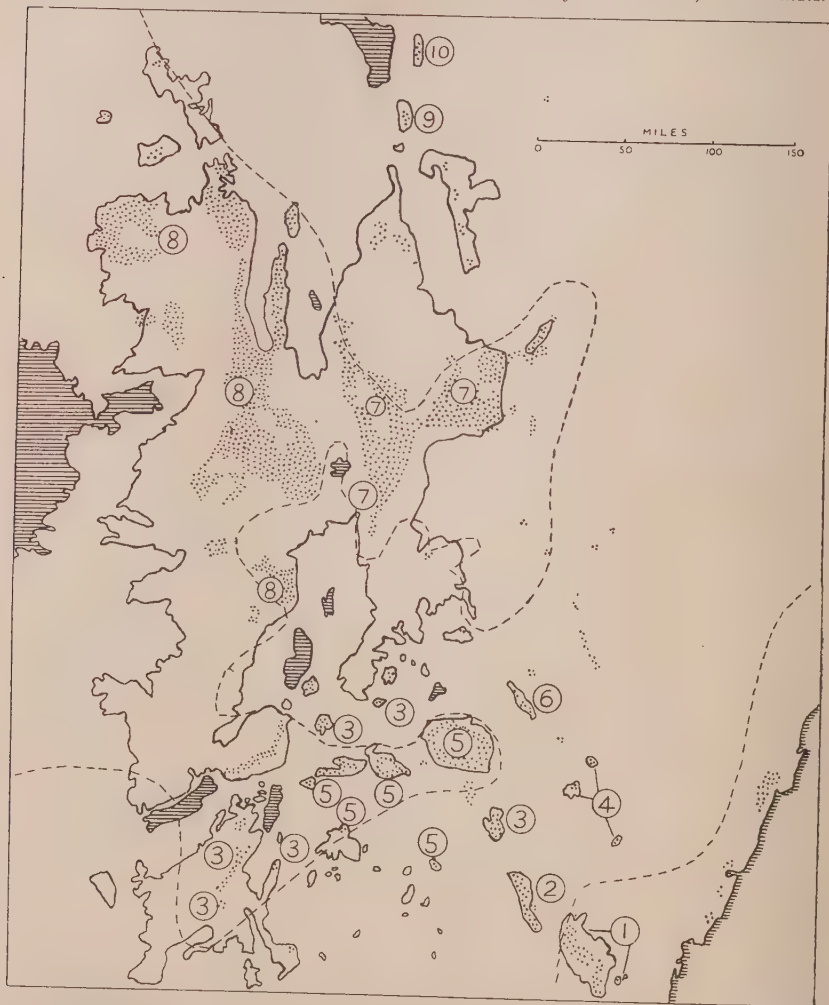


FIG. 2.—Sketch-map of Kenya Colony and northern Tanganyika Territory to show the distribution of (ten) different forms of montane-forest *Zosterops* within a distance of 600 miles.

The 5,000-foot contour is represented by a solid line, evergreen forest by dots. The broken lines are the isohyets of 30 inches of rain a year. *Zosterops* (2), (4) and (6) are surrounded by particularly dry country.

The foregoing particulars point to the following generalizations :—

A. The differentiation between the montane and the lowland-forest avifaunas is partly at the generic level and must be correspondingly ancient.

B. The distribution of many of the montane-forest bird-species is wide and covers indiscriminately both recent volcanic and ancient crystalline mountains. Several circumstances strongly suggest their dispersal as a group rather than their random dispersal.

C. This suggestion must be extended to cover also the widely isolated mountains of the Cameroons, but it does not apply to montanes in southern Africa (south of the Zambesi), nor to the Abyssinian highlands, where the forest avifauna seems more like the product of random dispersal.

D. Isolation between montane forests as little as a dozen miles apart in East Africa has been effective enough for a high degree of subspeciation.

E. The East African lowland-forest avifauna is well differentiated from the much richer West African at the specific level but not at the generic.

DISCUSSION.

The all-too-scanty data that we have on the state of Tertiary and Pleistocene Africa have been summarized and discussed elsewhere (Moreau, 1952 b). Unless otherwise indicated, statements made below are documented in that paper. It may be recalled that for birds fossil evidence is lacking and also that practically nothing is known about the condition of tropical Africa in the long and vital period of the Pliocene. However, at least the following conclusions appear to be justified :—

- (1) Since the Eocene the continent has been of much the same shape and size as at present. There has not at any time been an invasion of the sea that would provide more than one area, isolated by water, in which evolution could proceed independently.
- (2) Up to the Miocene the continent of Africa was tectonically quiescent, progressively degrading to a peneplain*, the general surface of which would not in its highest, central, part be sufficiently above the sea to rank as montane if the altitude-temperature correlation was the same as at present. Africa acquired its present diversified surface and high relief in the course of the Pliocene and Pleistocene.
- (3) Throughout most of the Tertiary the equator lay, subject to minor fluctuations (see below), near the middle of Africa, with the present sequence of climatic belts on either side of it, including a Saharan, much as now. The conception of an Africa completely covered with evergreen forest at any time is untenable.
- (4) Striking climatic fluctuations took place during the Pleistocene but their exact extent is not yet ascertained (see below). They are vouched for by a variety of geological evidence and contemporaneity over at least the area from northern Tanganyika Territory to Abyssinia has been claimed. It seems probable, but has not been proved, that the cooler and/or wetter phases in East Africa were contemporaneous with the glacial maxima of Eurasia. Nilsson (1952) has recently re-affirmed his belief that the Kageran, Kamasian and Gamblian pluvials were contemporaneous with the Mindel, Riss and Würm glaciations respectively; but Zeuner (1952 a) has advocated caution in accepting this correlation. If it were correct, it would, on Zeuner's (1952 b) dating of Pleistocene events, make the Kamasian about 180,000 to 230,000 years ago and the Gamblian about 115,000 to 22,000 years ago.

* *Pace* King (1951) ; see *Dixey* (1952).

- (5) Two factors will have been operating continuously to affect the local distribution of rainfall in tropical Africa, with results on a scale sufficient to develop and to extinguish ecological islands. One is the changes in heights of land, by erosion or by tectonic action, a by-product of which are changes in the penetration of the interior by moisture-laden winds. The other is the oscillations in the position of the caloric equator, calculated to reach up to 15° of latitude, but probably involving much smaller shifts in the situation of the climatic belts.

If these views are accepted, it follows that something like the present latitudinal range of climates would have been available in the continent throughout the Tertiary. However, in accordance with the trend of world-climate, the Tertiary temperatures were probably higher than the present, rather than lower, throughout Africa, at any rate in the earlier part of that epoch. This would have meant that in the tropics the development of montane conditions would have necessitated altitudes well above the present 5,000 ft.

If the equator lay near its present situation, then the associated belt of heavy and well-distributed rain would have provided the conditions necessary for lowland evergreen forest more or less across the centre of Africa throughout the Tertiary. It is problematical whether these conditions extended right across the continent or whether, as now, in the eastern side most of the interior was too dry to support evergreen forest at low altitudes. With a thoroughly developed peneplain the moisture-laden winds from the west would have been able to penetrate better to East Africa than they can at present. But the nature of the Miocene mammal fossils indicates that during that epoch, as now, savanna was present in Kenya as well as evergreen forest.

The extent of the affinities between the East African and the West African lowland-forest avifaunas, consisting of the same genera, but with a minority of species in common, is evidence for interchange between east and west at a period not very far back in the Tertiary. The evidence of the Kenya mammal fossils does not of course exclude the possibility of such interchange even in the Miocene, either by means of some corridor before the present mountain systems were fully developed or, indeed, at some stage in the 18,000,000 years of the Miocene that is not represented in the Kenya fossil beds. Certainly the nature of the differences between the eastern and the western avifaunas is what might be expected to result from a factor—the elaboration of the East African mountains—that must have become increasingly operative as a barrier through the Pliocene and the Pleistocene.

The difference between the East African lowland-forest avifauna and the West African is, as noted above, greater, though not above the specific level, than that between the Upper Guinean and the Lower Guinean (Congo) sections of the West African. There the difference is rather that the further western forests tend to be depauperate, yet without many endemic species. The present barrier, the savanna between about Lagos and Accra, is one that might have been reduced repeatedly during the Pleistocene, during a general pluvial or during a northward swing of the caloric equator. Two other barriers have been suggested (cf. Rand, 1951), namely, a northward extension of the sea before the development of the Niger Delta, and the extension of montane conditions to form a barrier, still narrow but more connected than at present, north from Cameroon Mt. during a pluvial (see also below). The three barriers mentioned would be operative in different parts of the 700 miles from Cameroon Mt. to Accra and each would be more impermanent than the barrier formed by the development of the East African highlands. In fact the main features of the geography of the lowland-forest avifauna of Africa seem fairly acceptably explained.

The problem of how and when the lowland- and the montane-forest avifaunas originated and became differentiated from each other is a baffling one. To start

with, areas suitable for lowland forest and montane forest respectively must be postulated, which were isolated from each other and from savanna geographically and/or were extensive enough to resist 'swamping' by genes from the other biomes. That the differentiation of the avifaunas dates from as early as the Miocene is suggested by the fact that, on fossil evidence in other parts of the world, many genera of birds are much older than that. For the evolution of the lowland-forest avifauna the prime conditions would be provided if an area like that of the Congo basin, with corresponding topography and climate, was available in the Tertiary; and there is every reason to believe that it was.

The origin of the montane avifauna is more difficult to envisage. There seems no reason to accept a hypothesis that it (and the rest of the montane biome) originally occupied the lowlands and was forced on to highlands by the incursion of the present lowland species (the provenance of which would set another problem). It is surely necessary to postulate for the evolution of the montane avifauna an area of montane climate of considerable size. This could have been situated either at a high enough latitude to have an approximation to a montane climate at low altitudes, thus *ipso facto* securing isolation from any lowland avifauna; or, if in the tropics, the nursery of the montane avifauna would have had to be on a highland.

The hypothesis of evolution well away from the equator is attended by the difficulty that both the areas that suggest themselves as suitable, the Abyssinian highlands and the area south of the Zambesi, are today excessively poor in montane-forest forms. The poverty of the Abyssinian montane in some groups other than birds has tentatively been attributed to local extinction as a result of volcanic activity and/or of Pleistocene glaciations (cf. Scott, 1952); but in a highland so large and of such varied topography this explanation is altogether inadequate to account for the avifaunal picture. So far as South Africa is concerned, it is conceivable that the great arid spell, tentatively dated to the end of the Pliocene, which extended the Kalahari Desert east over much of Northern and Southern Rhodesia, may have reduced the evergreen forest of southern Africa even further than the combined effects of a dry climatic cycle and man have done at the present day, with corresponding local extinction of forest forms. On the whole, then, South Africa is perhaps a more likely area than Abyssinia for the evolution of the montane-forest birds. It may be added that any suggestion of origin in the Palaearctic Region is disposed of by the fact that there are hardly any genera in common.

The other hypothesis, that these birds were evolved on an elevated area well within the tropics, leaves its location wide open to speculation. The great centrally situated mountain of Ruwenzori has been suggested, but its avifauna is no richer than that of the Kenya Highlands; and in any case the history of this massif is uncertain. Certain rock masses probably offered enough local resistance to the general process of peneplanation to form islands of montane conditions throughout the Tertiary but, except that the Ruanda highland (not distant from Ruwenzori) is believed by some geologists to have been persistently elevated above the progressively degraded general surface, their location and area are uncertain.

It is, of course, possible that the present montane avifauna is the product of evolution in more than one montane area, the species from which have subsequently, in a period of less difficult intercommunication, amalgamated to produce what we now see. Such a hypothesis complicates the problem of where the fields of montane evolution were situated; but certainly a period of intercommunication, altogether easier than at present, between different mountains must be postulated to account for the present wide, but inevitably discontinuous, range of so many montane forms. For interchange to be effective immense changes would be needed in the vegetation-cover of the low ground between the mountains. Semi-arid thornbush and savanna are inimical

to montane-forest birds and, as we have seen, lowland forest seems hardly less so. Consequently really free interchange could be secured only if montane conditions were brought right down into the lowlands. At least a tendency in this direction occurred during each Pleistocene pluvial and the crucial question is how far the change in climate (and vegetation) actually went.

The fact that the moraines on certain of the East African mountains were at one time 4,500 ft. lower than at present has sometimes been taken to indicate lowering of temperature by over 7° C., but the deduction is not sound. The mountains, being less degraded by erosion than at present, would have supported larger snowfields, and the greater size of the glaciers would therefore not necessarily connote a proportionately cooler or damper climate in tropical Africa generally. They were themselves too small to affect the general climate, as has been tentatively suggested: for example, the ice-cap on Elgon (14,000 ft., one of the highest East African mountains) covered only some 40 square miles and that on Simien in Abyssinia, 1,000 ft. higher and 11 degrees further from the equator, only 250 square miles (as calculated from the moraine maps in Nilsson, 1940). At the same time, if the glacial extensions on the various African mountains were contemporaneous, as seems probable from their sequences, they point to general changes in the climate of the inner tropical belt which are likely to have involved increased general cloudiness. This, irrespective of increased precipitation, would have made for a more humid climate. In any case, the East African pluvials may well have been contemporaneous with the major glaciations of the north, which, as Dr. C. E. P. Brooks points out to me (*in litt.*), have been calculated to occasion a world-wide cooling of as much as 5° C. That, if effective in the tropics, would have been equivalent to a lowering of the isotherms on the African mountains by 3,000 ft.*

Such a lowering of the isotherms could by itself have joined ecologically some of the montane areas now isolated from each other, and the more the lowering of the temperature was accompanied by increased precipitation, the more generally montane forest had a chance to expand. A lowering of the isotherms by 3,000 ft. would certainly have gone far to provide at least a good series of montane stepping-stones along the northern rim of the Congo Basin, which forms an arc between the mountains of the Cameroons and those of eastern Africa. The development of forest, in an area now so dry, would have been facilitated by any northward swing of the caloric equator. It is very doubtful whether a 3,000-foot difference in the isotherms sufficed to link up some of the mountains which are surrounded by particularly dry, hot thornbush, for example, the Teitas, Chyulus and Kisigau, and, most important, whether it would have bridged the gap past Lake Rudolf between the Abyssinian and the Kenya montanes. Any amelioration of the climate here might however have been assisted by the draining of a greatly enlarged Lake Rudolf north through the gap to the Nile Basin, for which there is evidence (cf. Worthington, 1952).

It follows from the above that intercommunication between the lower edges of many of the montane forests at least once during the Pleistocene is not difficult to envisage. It must, however, be recognized that the lowering of the montane limit by 3,000 ft., which suffices to meet some difficulties of bird-distribution, is quite insufficient to solve other problems. Unlike plants, the avifauna includes no species that are strictly confined to the upper parts

* The problem posed by the nature and the world-wide distribution of submarine canyons and other suggestions of great changes in the ocean bottom during the Pleistocene have forced some authors to postulate a world-wide fall in sea level amounting to many hundreds or several thousands of feet at least once during that period. Such a solution appears to raise many difficulties. If correct, there would have been an important effect on the temperatures of the land-masses, and those in the tropical highlands would have been lowered. See discussions, for example, by Malaise (1951), Shepard (1951, 1952), Landes (1952), Emery & Natland (1952).

of the montane forests, say over 9,000 ft., and no important moorland community (living above the timber-line*). But for any moorland organisms a lowering of isotherms by 3,000 ft. would do little to connect their isolated stations.

The extent of subspecific differentiation in neighbouring montane forests has a bearing on the provisional dating of intercommunication between them. If the last big East African pluvial, the Gamblian, is regarded as contemporaneous with the last, Würm, glaciation, it may have come to an end only some 22,000 years ago. It is certain that subspecies can develop in a shorter period than this (Mayr, 1942). Consequently the high degree of subspeciation between neighbouring East African mountains does not exclude the possibility that at least some of them were in communication in the Gamblian pluvial; and the fact that certain of the Cameroon montane birds are not differentiated from eastern ones would favour the acceptance of a late date.

In conclusion it is worth while to stress once again the enormous uncertainties that beset a discussion of this nature on Africa. There is, except for mammals, no fossil evidence. About Pliocene conditions on the continent we know practically nothing. The rates of evolution are particularly uncertain. And finally, at least so far as forest birds are concerned, there has been no complete systematic revision with particular reference to problems of distribution and evolution.

SUMMARY.

(1) The montane-forest avifauna differs nearly as much from the lowland-forest avifauna as it does from that of the ecologically very different savanna. Only about 12 per cent of the montane species occur regularly also in the lowland forest and a number of the montane genera are endemic.

(2) Many of the montane species are widespread on island mountains throughout East Africa, and half those on the mountains of the Cameroons occur also in the east; but remarkably few species reach the Abyssinian highlands or south of the Zambesi.

(3) Subspecific differentiation in montane species is often high, even on mountains within 20 miles of each other (example, *Zosterops*).

(4) The present geography of the forest birds is discussed in relation to what is known of Tertiary and Pleistocene Africa. The problem of how and where the montane and lowland-forest avifaunas were differentiated is baffling.

(5) The wide distribution of many montane species would have been facilitated by the Pleistocene pluvials and it is not inconceivable that the observed subspecific differentiation has taken place since the last of these.

(6) The difference between the Guinean forest avifauna and the poorer East African (coastal) lowland avifauna, with its high specific endemism, is explicable by the increasing barrier of the East African highlands during the Pliocene and Pleistocene. The difference between the Lower Guinean and Upper Guinean avifaunas is explicable on a combination of factors.

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* Only two birds are typical inhabitants of the moorlands: a chat, *Pinarochroa sordida*, on the highest mountains of Abyssinia, Kenya and northern Tanganyika Territory; and a sunbird, *Nectarinia johnstoni*, on Ruwenzori, the Kivu mountains, Kilimanjaro, Mt. Kenya and mountains around the north end of Lake Nyasa. Other birds occurring on the moorlands are obvious recent immigrants from lower down the slopes.

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NOTES ON THE RECENT AND FOSSIL MAMMALIAN FAUNAS OF AFRICA

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The earliest reference to the fossil mammals of Africa may well be buried somewhere in the voluminous writings of Olaus Borrichius (1626–1690), but serious study did not begin until about 1840. An annotated bibliography of the literature, now in the press, comprises nearly nine hundred titles and it is evident that a detailed summary of the results is not possible within the limits of this discussion. Nevertheless, a broader treatment may be of use to workers in other fields by suggesting something of the past history of the African biosphere, but it should be realized that, despite the extensive literature, we still know very little and that mammalian remains of Paleocene, Lower Eocene, Middle and Upper Oligocene, Middle and Upper Miocene, and of Pliocene age have not yet been found. Moreover, the localities whence fossil mammals have been obtained are widely scattered and few in number. Thus, Eocene deposits have been found in Egypt and Nigeria, Oligocene in

Egypt, and Miocene in Algeria, Egypt, Kenya, the Belgian Congo and South-West Africa. Only Pleistocene deposits are at all widely distributed; even so, the number of localities is small in relation to the size of the continent.

The fossil mammals of the Eocene deposits are nearly all archæocete whales, more commonly known as zeuglodonts, but there is one terrestrial genus, the primitive proboscidean *Moeritherium*. Thus at the very beginning of the record a characteristic African faunal element is present.

The Lower Oligocene fauna is wholly terrestrial and much richer than its predecessor. It contains Proboscidea, Hyracoidea, *Arsinoitherium* and *Barytherium*, all of African origin, as well as anthracotheres and hyænodont carnivores, the former of European and the latter of North American origin. This fauna also contains the earliest known Old World monkeys, namely, *Moeripithecus* and *Apidium*, members of the Cercopithecidae, and *Proplioptithecus*, a primitive gibbon. The assumption that the Cercopithecoida and Hominoidea are of African origin is based on these fossils.

There is no evidence of the course of events during the remainder of Oligocene times, but the composition of the Lower Miocene fauna confirms the inference from general principles that some forms would have died out while others continued to evolve, and these latter would have been joined by immigrants from regions outside Africa. Thus *Arsinoitherium*, *Barytherium*, and *Moeritherium* became extinct and left no descendants, and the anthracotheres survived but little changed, but the Proboscidea and the Primates continued a rapid evolutionary radiation and also colonized extra-African areas.

Among the new appearances in the Lower Miocene fauna, an aard-vark and one or two genera of golden moles (Chrysochloridae) are typically African: the former is represented by an isolated tooth found at Koru, Kenya, in 1931, and by other remains found at Mwangano, Kenya, at a later date; the latter are known by a few skulls found at Koru and on Rusinga Island. Immigrant forms are represented by chalicotheres and rhinoceroses, both of them apparently of Asiatic origin. Another new group to appear in the Lower Miocene is that of the ruminants, represented by the primitive antelope *Eotragus* and more than one genus of chevrotain (Tragulidae). *Eotragus* has previously been found in European deposits of Upper Miocene age; that it should occur in East Africa in Lower Miocene deposits suggests its African origin, with the further implication that the whole of the Bovoidea may also have originated there.

There are numerous references in the literature to North African faunulæ of Pliocene age, but only two of them, one in Morocco, the other in Tunisia, seem likely to be confirmed. For the moment it is broadly true to say that the Pliocene fauna is not known.

At the opening of Pleistocene times, the Sahara, that vast barrier to migration, did not exist and to that fortunate circumstance we owe the possibility of establishing the Villafranchian date of the earliest Pleistocene deposits to the South of the desert belt. In the North, along the Mediterranean coast, the terrestrial beds interdigitate with marine deposits of Calabrian age. The Calabrian is the marine equivalent of the Villafranchian, therefore the fossils found in the interdigitating beds must be of Villafranchian age. The most important fossils are a mastodont comparable with *Anancus arvernensis* of the Villafranchian of Europe, an elephant closely allied to *Archidiskodon planipons* of India, and *Libytherium*, a member of the giraffe family characterized by its short legs, heavy skull, large palmate horns, and thick neck. It is but little different from the Indian genus *Sivatherium*. Both the Indian forms occur in the Pinjor zone, long recognized as the equivalent of the European Villafranchian; thus the North African deposits may be dated by their stratigraphy as well as by their palæontology. Because there was no desert

barrier, this fauna, with regional variations, was able to maintain itself all over the continent: it has been discovered in southern Abyssinia, at Kaiso in Uganda, at Kanam in Kenya, in Tanganyika, in the 80 ft. terraces of the Vaal River, and there are good grounds for believing that it occurred in the Belgian Congo. Survivals from the Pliocene are represented by the sivatheriine genera *Griquatherium*, *Libytherium*, *Sivatherium*, the aberrant proboscidean *Deinotherium*, chalicotheres, and three-toed horses closely allied to, or identical with, the European genus *Hipparion*. Possible new arrivals include many antelopes (e.g. *Kobus*, *Alcelaphus*, *Damaliscus*) and the bush pigs and wart-hogs (*Koivopotamus*, *Phacochoerus*), all apparently of Asiatic origin.

With the development of the Sahara, the area of distribution of the Villafranchian fauna was divided into a smaller Northern section and a larger Southern one. This gradual, intermittent, but cumulative process continued for a very long time, and the North was not isolated from the South before the end of the Middle Pleistocene. The faunal changes in French North Africa have been studied in some detail. Joleaud summarized them thus:

(a) The giraffe and *Libytherium maurusium* persisted in Barbary until the end of the chelleo-acheulean cultures.

(b) *Elephas atlanticus*, *Rhinoceros mercki*, hippopotamus, *Oryx algazel*, *Bubalus antiquus*, eland, *Gazella dama* were either greatly reduced in numbers or else had disappeared from Barbary by the end of the moustesian cultures.

(c) Wart-hog, gnu, roan antelope, and *Lycaon* persisted for a longer time and may have been contemporary with mesolithic cultures.

At a later date many species were still living in Tripolitania and the central Sahara. The times of their disappearance were approximately

(1) 2,000–1,500 B.C. Rhinoceros, buffalo, hippopotamus.

(2) 1,500–500 B.C. Giraffe.

(3) 500–300 B.C. Elephant, horse, ox.

The sequence of events in Central Africa was similar, and there is already sufficient evidence to warrant a tentative summary, thus:

(a) Lower Pleistocene. *Stegodon*, machairodonts, and hippopotamuses of the *H. imaguncula* type did not survive the pre-chellean cultures.

(b) Middle Pleistocene. *Deinotherium*, *Anancus*, and chalicotheres in the lower part, and *Elephas recki*, *Sivatherium*, *Stylohipparion*, *Pelorovis*, and *Bularchus* in the upper part, died out with the chelleo-acheulean and acheulean cultures respectively.

(c) The Upper Pleistocene is still insufficiently known for any certain conclusions to be drawn from the few facts available, but it would appear that the present fauna was fully established, even though the distribution of the species may have been different.

The majority of the South African fossils, apart from those of the terraces of the Vaal River, have been obtained from caves, but the contents of the river terraces seem to show faunal breaks that correspond to those of Central and North Africa.

Greater difficulty is encountered when one attempts to trace the history of the elements composing the present fauna and of their distribution. Some genera and species, such as giraffe, hippopotamus, striped and spotted hyaenas, black and white rhinoceroses, were already present at the end of the Pliocene or soon after. Throughout the Lower and Middle Pleistocene the white rhinoceros (*Ceratotherium sinum*) was common all over Africa, whereas the black species (*Diceros bicornis*) was rare: from the Upper Pleistocene onward

the position was reversed. The African elephant is absent from all deposits earlier than the very latest Pleistocene, neither is there at present any indication of its probable place of origin.

The changes in fauna coincided with changes in climate and concomitant changes in flora. Pluvial periods allowed the forests to increase, whereas interpluvial periods, being drier, were favourable to the spread of grassland, but the general tendency appears to have been towards ever-increasing dryness. Fully to understand the effect of climatic change is not possible; not only is information concerning the past quite insufficient, but there is a grievous deficiency of knowledge of the ecology of the Recent fauna and flora.

As an example of the kind of problem that often arises, the replacement of *Alcelaphus* by *Damaliscus* in certain deposits of Pleistocene age in the Belgian Congo may be cited. At the present day *Alcelaphus* is unknown in the area in question, whereas *Damaliscus* is relatively common. Both genera inhabit short-grass country as a rule and do not willingly enter tall grass or scrub, but there is some evidence to suggest that *Damaliscus* will tolerate rather less open country more readily than *Alcelaphus*. When one remembers what great floral changes may accompany an increase or decrease in annual rainfall of only a few millimetres, one realizes that even a small climatic change might so affect the vegetation that one species could migrate to regions that were still inaccessible to the other.

To conclude. Much work has been done on the Recent and fossil mammals of Africa, but much more remains to be done. The most pressing needs from the point of view of the student of Pleistocene faunas are studies of the distribution of the Recent species of mammals in relation to the flora, and of plant distribution in relation to rainfall, especially in relation to small differences of rainfall.

THE DISTRIBUTION OF SOME AFRICAN MOSQUITOES

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(With 5 text-figures.)

By reason of their medical importance the African mosquitoes have now been studied more or less intensively for about fifty years. During this time very large numbers of distribution records have accumulated but until recently little attempt has been made to assemble and collate these and to interpret them in terms of the relationship of the various species to their environment. For this reason my remarks will be based mainly on the subgenus *Stegomyia* or *Aedes*, on which I have already published in some detail (Mattingly, 1952, 1953) and the subgenus *Culex* sensu stricto which is the subject of a current study. I shall also have occasion to mention a few species of the subgenus *Neoculex* of *Culex* and of the subgenera *Aëdimorphus* and *Ochlerotatus* of *Aedes*, although the distribution of most of the species included in these subgenera has still to be worked out.

For the purposes of my own approach I have sorted the problems of African biogeography roughly into three groups, those concerning the present distribution of the mosquito fauna and the factors by which it is maintained, those concerning the origins of the present distribution and the factors which have brought it about, and those concerning the distribution of recently introduced species, more especially those introduced by man.

In connection with the first group of problems I shall confine myself to *Stegomyia* and shall try to relate the distribution of its constituent species on

the one hand to such empirical climatic limits as can be deduced from the available data and on the other to the zoogeographical sub-regions and districts devised by Chapin (1932) for the birds. In general, Chapin's faunal districts seem to serve very well for the mosquitoes, although I should like to see them amended in detail.

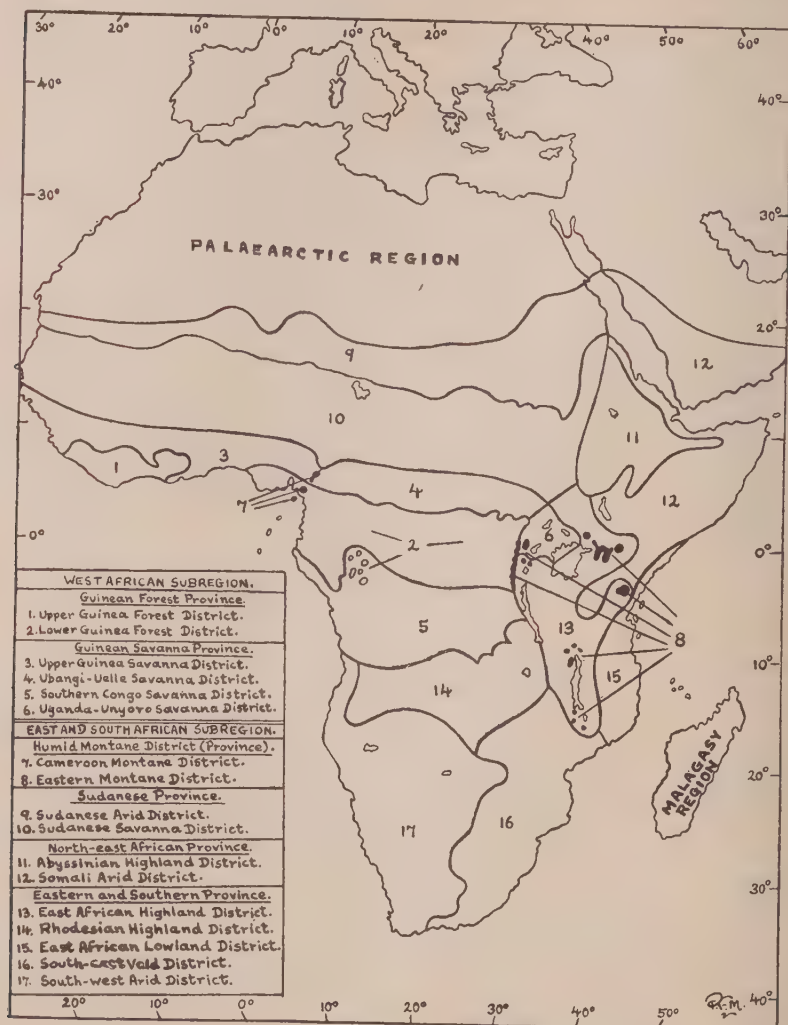


FIG. 1.—Faunal areas of Africa south of the Sahara after Chapin.

Chapin's West African Sub-region (fig. 1) is wholly occupied by only two species of *Stegomyia*, *Aëdes* (*S.*) *africanus*, the principal vector of endemic forest yellow fever in Africa, and *Aëdes* (*S.*) *apicoargenteus*. A number of other species occur in the peripheral savannas and woodlands but are excluded from the great central blocks of forest, the Upper and Lower Guinea Forest Districts, by their inability to penetrate dense forest of this kind, a failing common to very many animals which imposes on the fauna of these districts

a somewhat impoverished character, at least as regards variety of species. The only species, other than the two already mentioned, which occur in the Forest Districts at all are *Aedes* (S.) *egypti* and *Aedes* (S.) *simpsoni*, the principal vectors of town and rural or plantation yellow fever respectively, and *Aedes* (S.) *vittatus*. Of these the first two have been introduced by man, *Aë. simpsoni* in the axils of broad-leaved food plants which constitute its principal breeding-places, and occur only in artificially cleared areas. *Aë. vittatus* is restricted to areas of older (pre-Karoo) rocks in the north-east and, since it is primarily a rock-hole breeder, it seems evident that its limits are at least partly geological (fig. 2).

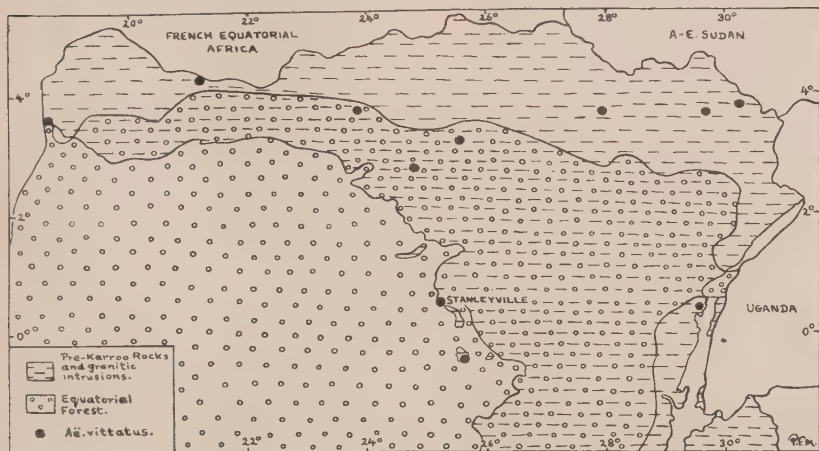


FIG. 2.—Distribution of *Aedes vittatus* in the northern Belgian Congo. Elsewhere in the Congo this species is known only from the Katanga and the region below Leopoldville, both areas of ancient pre-Karoo rocks. The geological and vegetational boundaries are taken from the appropriate maps in the Atlas Général du Congo.

In the northern part of their joint range both *Aedes africanus* and *Aedes apicoargenteus* have been found for some distance beyond the boundary of the western sub-region as defined by Chapin. In this area their distribution appears to be closely defined by the 40 in. isohyet and I should be inclined to take this isohyet as the natural boundary of the sub-region subject to some modification to allow for the seasonal distribution of rain expressed in terms of the length of dry season. To the north-east the limit is clearly an altitudinal one and here again both species transgress the limits set by Chapin, being found in the forests of the Central Kavirondo referred to on p. 28 by Milne-Redhead and on Ukara Island at the southern end of Lake Victoria. Here I would take the boundary of the sub-region as the 5,500 ft. contour on the western face of the Kenya highlands, then westwards and northwards parallel with the edge of the lake to the level of Bukoba. From here it should be continued rather further north than Chapin takes it around the dry tongue centred on Mbarara (fig. 3). Southwards from here to Albertville the boundary is, as Chapin indicates, mainly an altitudinal one and the same contour (5,500 ft.) would probably serve, but south-westwards along the face of the Rhodesian plateau conditions alter radically. In the Central Kavirondo *Aedes apicoargenteus* ascends, as far as we know, to about 5,500 ft. but *Aedes africanus* appears to go rather further, up to about 6,000 ft., and it is most interesting to find that the same slight difference in altitudinal tolerance still holds when the Rhodesian plateau is reached, for here *Aedes apicoargenteus* passes out

at about 3,500 ft., being replaced above this altitude by a distinct though closely related species, *Aedes schwetzi*, while *Aedes africanus* carries on up onto the plateau and so is enabled to spread down into Northern Rhodesia, its southern limit being now a rainfall one. There is indeed evidence that at one time it spread still further southwards and eastwards because there are old records indicating the occurrence of relict populations in the wet forested areas around Zomba and in northern Mozambique. For all I know to the contrary it is there still.

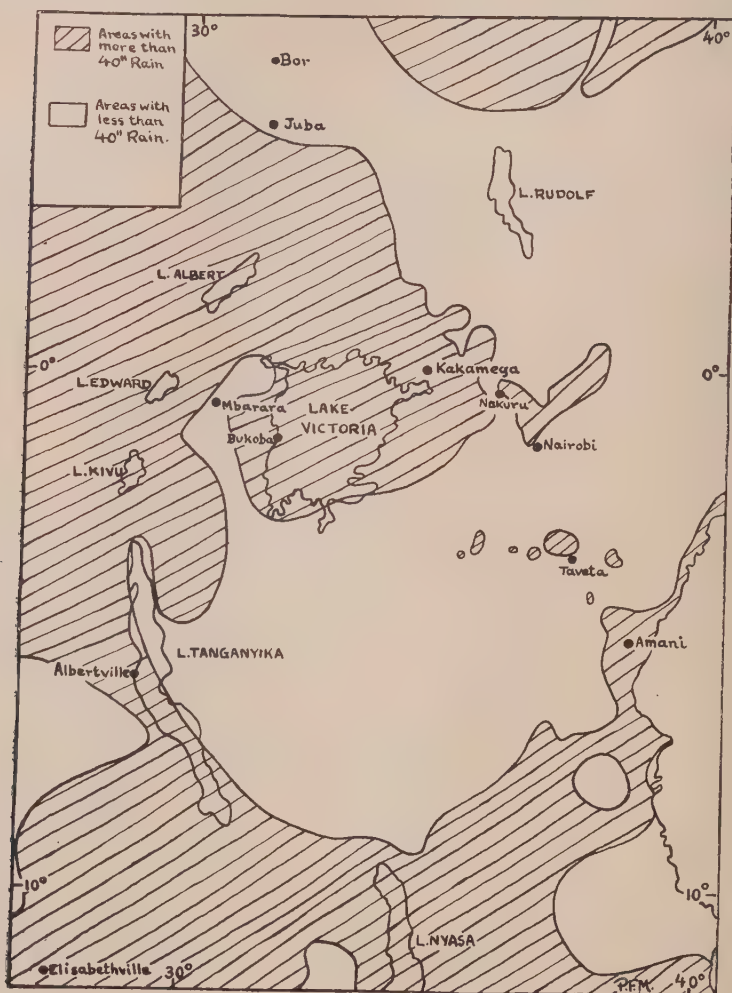


FIG. 3.—Mean annual rainfall in East Africa, based on East African Forces Map No. 1518.

Northwards from here another relict population of *Aedes africanus* has been discovered far eastwards from its main range at Taveta in Kenya. This record is of particular interest, since it throws considerable light on the significance of rainfall in determining distribution. It might be thought that the

limiting factor in the case of a tree-hole breeder, such as the present species, would be the availability of sufficient rain to fill the breeding-places, but it is probable that in general the rainfall limit of forest *Stegomyia*, though not perhaps of those of the savanna, is well above this requirement. At Taveta the mean annual rainfall is about 26 in., which is, as we have seen, far below the normal requirement of *Aedes africanus*. That this species is able, nevertheless, to maintain itself in the area is apparently due to the presence of a very high subsoil water-table, caused by drainage from Kilimanjaro, which supports a dense, humid forest of equatorial type. Thus while the local rainfall is sufficient to fill the breeding-places, at least under forest conditions, the abnormal subsoil water-level, of extraneous origin, ensures the optimal microclimate which the forest affords.

Before leaving *Aedes africanus* mention must be made of the occurrence of isolated populations of this species in the two main humid areas of Abyssinia. The occurrence of a large West African element in the Abyssinian fauna is one of the classical problems of African zoogeography and it is felt that a study of the climatic limits of the mosquitoes concerned can probably shed some light on how they got there. Much of the relatively dry area which now separates the humid regions of Abyssinia from those of Central Africa has a rainfall of 30-40 in. with five dry months (months with less than an inch of rain) in the year and the evidence suggests that this is too little for *Aedes africanus*, at least in the absence of special factors such as those discussed above. Eastwards from the line Bor-Juba, however, a broad belt apparently exists having an annual rainfall of about 35 in. with only three to four dry months in the year. Although such a rainfall is probably just too low for *Ae. africanus* under most conditions, I should regard it as marginal, and it seems to me evident that this species could have crossed from the Central African forests into Abyssinia with only a very slight increase in rainfall. It is also interesting to note that the map (NB 36 of the international series) shows small patches of relict forest in the little-known area of the Sudan, which the belt to which I have referred traverses (see Mattingly, 1953, fig. 14).

Turning to the West African savannas we again find two characteristic species, *Aedes* (S.) *fraseri* and *Aedes* (S.) *dendrophilus*. The first of these is apparently restricted to the northern savannas, as delimited by Chapin, except that it occurs in the forests of the Central Kavirondo, a further reason for treating these forests as a part of the Uganda-Unyoro Savanna District, as I have suggested above. The second species, *Aedes dendrophilus* has a wider distribution and has recently been found in certain forests in the Katanga, near Elisabethville, an indication that it probably occurs also in the Southern Congo Savanna District, which has so far not been very thoroughly explored. In the northern savannas both *Aedes fraseri* and *Aedes dendrophilus* appear to be restricted by the 40 in. isohyet in much the same way as *Aedes africanus* and *Aedes apicoargenteus*. That they do not, like these species, extend out into the adjacent Sudanese Savanna appears to be due to their much more limited tolerance of a long dry season. In the Guinean, Ubangi-Uelle and Uganda Unyoro savannas they have to contend with a dry season of only about three months or less. It will be seen from this that the record of *Aedes dendrophilus* from Elisabethville is very exceptional, since this area has about six dry months. The explanation is again apparently identical with that adduced to explain the presence of *Aedes africanus* at Taveta, namely, the occurrence of an exceptionally high local subsoil water-table. Thus in the Elisabethville area *Aedes dendrophilus* has only been found in forests of a special type occurring at the sources of streams and small rivers. By reason of the abundant subsoil water at such points these forests (known in the Katanga as Muhulu and in different parts of Northern Rhodesia as Mushitu, Itu or Litu) are much denser and more humid than the ordinary gallery forests occurring

lower down the rivers. Their recent exploration has added to the Katanga mosquito fauna a large number of West African species not previously suspected to occur there.

Much more remarkable than the occurrence of *Aedes dendrophilus* in the Katanga is the occurrence of an isolated population of this same species in South Africa. Here it is found in the area of high rainfall running along the coast from Zululand in the north to Pondoland in the south. Chapin has noted the occurrence of some West African groups of birds in this area and has suggested that the southern forests which they inhabit must at some time have been continuous with those of the West African Sub-region. With this I am in agreement, provided it is realized that complete continuity need not have existed at any one time. All that is required is that the various intermediate forested areas which still occur should in turn have been connected to one or other of their neighbours, thus providing a series of stepping-stones from north to south or vice versa over a period of time. The coastal forests and woodlands of Zululand, Natal and Pondoland have precisely the same type of rainfall as that already noted as suitable for *Aedes dendrophilus* in the West African savannas, i.e. a mean annual rainfall of about 40–50 in. with a dry season of one to three months. In an earlier paper (Mattingly, 1952) I mapped a number of areas in southern and eastern Africa with a similar type of rainfall and I am glad to be able to record that *Aedes dendrophilus* has since been found in one of these, in the coastal lowlands of Kenya and at Amani.

Before leaving the West African Sub-region mention must be made of the dry gap between the Upper and Lower Guinean Forests, to which attention has been drawn by Milne-Redhead. This is the site of a remarkable rainfall inversion, so that between Lagos and Cape Three Points it is actually drier along the coast than it is further inland (see rainfall maps in Nash, 1948). Similar conditions prevail further south from a point north of the mouth of the Congo to somewhere above Capetown and a most interesting species of *Stegomyia* has recently been found in both areas (at Lagos and at Banana respectively). This is a mangrove species almost indistinguishable in outward appearance from *Aedes africanus* but with male terminalia showing a most remarkable resemblance to those of *Aedes fraseri*. It seems possible that it may have originated from hybridization between the two latter species, particularly as *Aedes fraseri* has recently been found breeding in mangrove, but at the same time I think it likely that geographical isolation has played a part in its evolution in the normal way. At Lagos it comes into close contact with *Aedes africanus* and I have myself taken them together, but it seems likely that at Banana, owing to the rather more rigorous rainfall conditions, the two may be isolated at the present time. The amount of precipitation in these coastal areas seems to depend largely on the direction of the coastline relative to that of the rain-bearing winds and it seems to me likely that in the past very small changes in coastal elevation (and so in the direction of the coastline) may well have sufficed to isolate the mangrove forests from the savanna woodlands further inland.

The remaining West African *Stegomyia*, *Aedes* (S.) *luteocephalus*, *metallicus* and *unilineatus*, are species of the Sudanese and other eastern and southern savannas which penetrate to varying degrees into the West African savannas, *Aedes luteocephalus* and *Aedes unilineatus* extensively, *Aedes metallicus* hardly at all. The detailed distribution of *Aedes luteocephalus*, a close relative of *Aedes africanus*, appears to be explicable largely on the basis of a refusal to enter closed forest. This refusal is very marked and has been directly observed in the field. In the case of the other two species, however, there appears to be a rather definite upper rainfall limit. Why this should be, our present knowledge of the ecology of these species is insufficient to explain.

The mosquito fauna of the East and South African Sub-region is not yet so well known as that of the western sub-region but already enough is known about it to justify some tentative conclusions of general interest. Three montane species are known from the western part of the East African Highland District, *Aedes ruwenzori*, a relative of *Aedes africanus* which is apparently confined to the Ruwenzori Range and *Aedes angustus* and *bambusae* which occur in bamboo forests in the Kigezi-Kivu area. Further east, in the western part of the Kenya highlands, *Aedes bambusae* is represented by a closely allied species or subspecies, *Aedes bambusae kenyae*, which extends down from about 10,000 ft. at the Equator into the Central Kavirondo forests, already mentioned, at about 5,500 ft. A certain number of other East African Highland mosquitoes are also found in these forests but the preponderance of West African species appears to be great enough to justify their inclusion in the western sub-region. The factor which restricts *Aedes bambusae kenyae* to the western part of the Kenya highlands and prevents it from extending into, for example, the Nairobi area, seems quite clearly to be rainfall, the 40 in. isohyet again forming a good approximate boundary (see fig. 3 above and fig. 6, Mattingly, 1953). Further east it is replaced in the drier part of the highlands by another close relative, *Aedes deboeri*. The distributional limits of the latter are not known but it is very probable that, where there is sufficient rain, it extends down to about 3,500 ft., since the distribution of other species of *Stegomyia* indicates that the dividing line between the East African Highland and the East African Lowland Districts lies at about this altitude (compare the boundary between the Southern Congo Savanna and the Rhodesian Highland Districts deduced above and see Moreau's remarks on the birds of the East African coastal region on p. 38).

Were our knowledge entirely restricted to Kenya the two remaining East African Highland species would appear to have very similar distributions but a consideration of their distribution and that of their near relatives elsewhere shows them to represent quite different elements in the fauna. One of them, *Aedes langata*, has been found from the Nairobi area southwards as far as the southern end of the eastern highlands of S. Rhodesia (Ndanga area). On the plateau of S. Rhodesia it overlaps with a close relative, *Aedes contiguus*, which continues on further south into the Transvaal and is in turn replaced by a third relative, *Aedes powerei*, occurring right down to the Tzitzikama Mountains nearly at the southern limit of the continent. The other species, *Aedes keniensis*, extends down to the northern foothills of the Livingstone Mountains and is replaced westwards from here by a relative, *Aedes masseyi*, in the Katanga. In its turn this species is replaced by a third, *Aedes amaltheus*, in the Zambesi valley, which from all its outward features would seem almost certainly to be a close relative.

This latter species is, however, one of the most remarkable of the African *Stegomyia*, for while in external characters it is, like *Aedes masseyi*, a perfectly typical member of the well-defined African group (Group A), it possesses highly distinctive male terminalia which are equally characteristic of the Oriental and Australasian group (Group C), which includes *Aedes unilineatus*. The latter occurs, as has already been stated, in the Sudanese savannas and also, probably as an isolated population, in the Zambesi Valley. It is also known from western India and has a close relative in Crete, Macedonia and the Black Sea area (*Aë. cretinus*). It is the only member of group C occurring on the African mainland. It seems probable that its upper limits (apparently about 3,500 ft.) correspond roughly to the present lower limits of *Aedes masseyi* and whether or not the two overlap at the present time they must almost certainly have done so in the recent past. On distributional grounds therefore, it seems quite possible that *Aedes amaltheus* may represent a *masseyi-unilineatus* hybrid. Alternatively it is possible that it is a genuinely primitive anectant species and

some weight is given to this hypothesis by the fact that its larva possesses certain distinctly primitive features. If this second alternative is accepted then I think we must assume that a main centre of differentiation and radiation of the subgenus as a whole has lain in this part of Africa. At the present time, however, there is not, in my opinion, sufficient evidence to decide. Some light would undoubtedly be thrown by genetical and cross-breeding experiments could someone be found to undertake these and it is possible that more will be shed by the discovery of the male of *Aedes masseyi* which is, at present, still unknown.

It has been indicated that the African group of *Stegomyia* (Group A) is a very distinct one with respect both to colour characters and the structural characters of the male terminalia. It includes all the African mainland *Stegomyia* except *Aedes unilineatus* (Group C) and *Aedes vittatus* (Group D) and it contains only one species, *Aedes chemulpoensis*, which occurs outside Africa. It is therefore very remarkable to find that this species is restricted at the present time to an area far away in North-east Asia embracing Pekin, Mukden and North-western Korea. This area corresponds so closely to the eastern glacial wooded refuge pictured by Reinig (1937, and see De Beaufort, 1951) that we must, I think, picture a considerable northerly, trans-alpine extension of Group A in pre-glacial times. The principal factor responsible for confining the bulk of the group to trans-saharan Africa would be the desiccation which accompanied the advance of the ice-sheets and which has left its mark in the broad belts of Loess soils lying immediately to the northward of the Alps and the Himalayas. Nor do I think we can altogether afford to neglect the very distinctive western Mediterranean fauna, which Reinig, De Beaufort and others have shown to have such strong connections with the eastern Asian refuge. De Beaufort quotes some striking cases of higher animals now restricted to this area but having all or most of their surviving relatives in eastern Asia and other cases will be found in Schmidt & Allee, 1951 and elsewhere.

A species of mosquito having this type of distribution and found also in Africa south of the Sahara is *Aedes vittatus*, which has already been mentioned. In Africa south of the Sahara this species is very widespread and it also occurs over most of the western Mediterranean area, including the eastern part of the French Pyrenees (*vide* Hamon, previously unpublished), Spain, the Tell of Algeria, the Balearic Islands, Corsica and Sardinia, while another isolated population is found occupying a large part of India and extending eastwards from there into Annam. It is, however, entirely absent from the eastern Mediterranean.

Another interesting case of a western Mediterranean species with trans-saharan affinities is that of *Culex brumpti* Galliard. This species is restricted so far as is known, to Corsica, but its closest, and indeed its only known close relative, *Culex zombaensis* Theobald, is widely distributed in the East African Highland District. The most instructive case of all is, however, that of *Culex univittatus* Theobald which has both eastern and western Mediterranean forms (fig. 4). The eastern Mediterranean form (corresponding to *Culex perexiguus* Theobald) extends throughout North Africa, far down into the Sudanese Savanna District, and eastwards through Palestine to North-west India. The western form is known at present only from southern Spain, though it doubtless occurs also in the Tell of Algeria. It agrees very closely with the type form which occurs widely in the savannas of tropical Africa. In the drier parts of tropical Africa intermediates occur (fig. 5). The distribution of these forms is, in general, very closely related to rainfall, sometimes strikingly so and this suggests that they are probably climatypes. There are, however, some notable exceptions, as may be seen from fig. 4, and until these can be explained the taxonomic status of the forms in question must remain in doubt. It seems likely that the matter could be cleared up if it were possible to take account

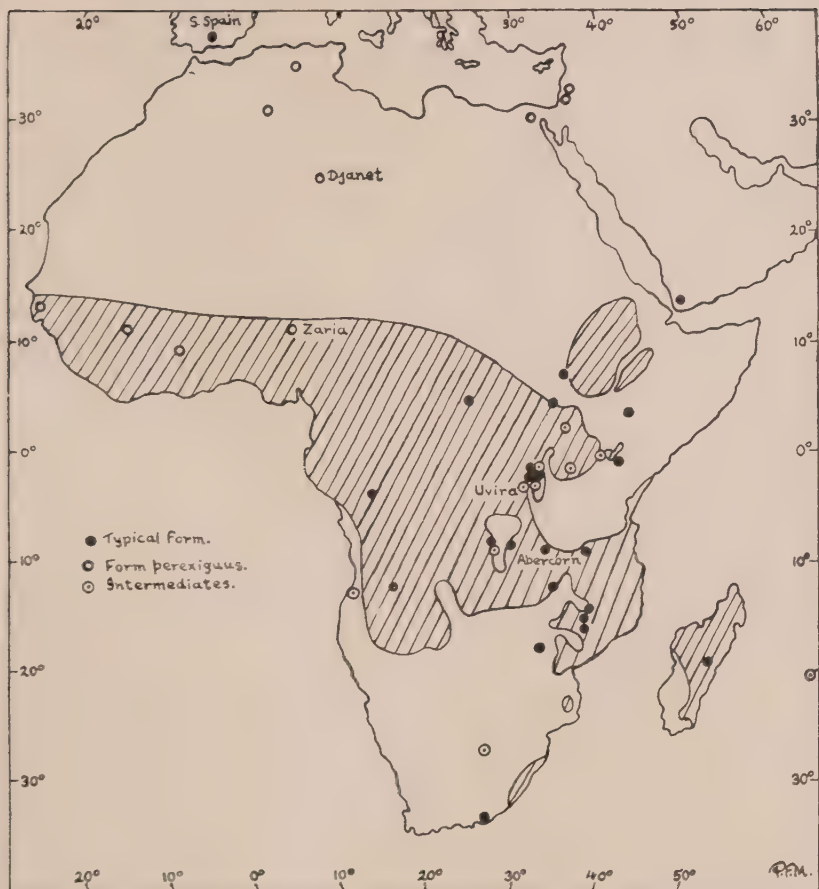


FIG. 4.—Distribution of *Culex univittatus*. Form *perexiguus* also occurs in North-west India.



FIG. 5.—Geographical variation in the spine on the ventral lobe of the phallosome of *Culex univittatus* Theo. For localities see fig. 4.

of temperature, but the temperature figures so far published for localities in tropical Africa are inadequate for the purpose, being very much less abundant than those available for rainfall. For the present purpose all that it is desired to stress is the much closer resemblance of the western Mediterranean form to that occurring in Central Africa than to the form occurring in between.

A comparable species is *Culex theileri* Theobald which occurs in the Canary Islands and all round the Mediterranean, and eastwards into northern Assam and Burma. In tropical Africa, however, it is confined, unlike *C. univittatus*, to the eastern and southern sub-region where it extends right down into Cape Province. The details of its geographical variation have not yet been investigated. *Theobaldia longiareolata* Macquart has a similar distribution but this species has succeeded in pushing northwards along the Rhône Valley and has been found in recent years on the south coast of England in the Portsmouth area, although it is not known whether it has become established there.* Of the two known members of the *Culex deserticola* group, *C. (Neoculex) deserticola* Kirkpatrick has been found, like *C. univittatus*, in the central Sahara and is widely distributed in Mediterranean Africa. Its close relative *C. (N.) salisburyensis* Theobald has been found on the Jebel Marra and, very recently, in South-west Arabia. Its main range extends from the southern Sudan through Kenya, the Katanga, the Rhodesias, the Transvaal and Natal into Cape Province. The most southerly form of this species shows some differentiation but the requisite material, in particular topotypic males, is lacking to determine its precise taxonomic status. In contrast to the geographical discontinuity of these two species may be mentioned *Culex (Culex) poicilipes* Theobald which occurs widely in Africa south of the Sahara and apparently has a continuous northern extension through the Sudan and down the Nile Valley to Alexandria, though it does not occur elsewhere in North Africa.

All these are examples of wide distributions but cases can also be found, in this genus, of very restricted distributions and wide discontinuities. Thus *Culex (Neoculex) arbienei* Salem has at present been found only in southern Sinai and on the Jebel Marra, and a newly discovered *Neoculex* from South-west Arabia has been found to have a subspecies in the Canary Islands.

Other species show interesting distributions in relation to the boundaries of the Ethiopian Region of the zoogeographers. Thus *Culex (Barraudius) pusillus* Macquart, which occurs in North Africa and the Near East, extends southwards in Egypt to within only a mile or two of the line normally taken as the northern boundary of the Ethiopian Region but has never been found beyond it. *Anopheles sergenti* Theobald, on the other hand, does penetrate beyond the eastern boundary of the region for some distance in southern Arabia, but for most of its range it appears to skirt the boundary, extending up into Palestine and eastwards from there to North-west India and westwards right across North Africa to the Canary Islands.

Finally, as an introduction to the problem of the origins of the modern subgenera of *Culex*, mention must be made of *Culex (Culex) laticinctus* Edwards. This species occurs in the Canary Islands, all round the Mediterranean and in South-west Arabia. In Africa south of the Sahara it occurs in the Sudan, Abyssinia and the Somalilands and it penetrates into Kenya as far as the Nairobi area. It appears to be related to a very interesting species recently found for the first time in the high Yemen. This species exhibits very bizarre modifications of the male terminalia which, in the Old World, are characteristic of a small group of species found in certain areas of recent volcanic activity. These areas are the Yemen, the Nakuru area of Kenya, the Aberdares, the Virungas and the Ruwenzori Range and certain very remote Pacific islands of the Society and Marquesas groups. The Pacific species, of which

* Since going to press it has been found in abundance at Epsom. This almost certainly indicates a recent progressive extension of its range.

two have so far been discovered, one very recently, show a close general resemblance to *Culex laticinctus* and its relative from the Yemen in the structure of the phallosome which has, however, in their case annectent features to other subgenera of *Culex*, notably *Neoculex* and *Culiciomyia*. They also show certain characters of ornamentation annectent to *Culiciomyia*. In the two species from the Nakuru area, on the other hand, the phallosome is radically different in structure. The group as a whole has interesting affinities with certain New World subgenera, including an Andean and temperate South American one. The *Culex pipiens* group *sensu strictissimo*, which is discussed more fully below, is perhaps best regarded as a third section of the subgenus. Its affinities seem rather to be with the Nakuru species than with the Arabian and Pacific ones, but its (apparently) most primitive member occurs in south-eastern Australia. An isolated member of the group also occurs on the volcanic island of Sao Thome in the Gulf of Guinea. The study of the zoogeography of this very interesting subgenus has only just begun and it is too soon to start drawing conclusions regarding its origins and evolution. In comparing it with *Stegomyia*, however, it does seem reasonable to suggest that any ancient centres of radiation which may have occurred are likely to have been situated in the southern rather than in the northern hemisphere.

Culex laticinctus is, in the main, a species of arid or semi-arid country and as such it must frequently be compelled to utilize breeding waters having, on the one hand, a high temperature and, on the other, a high mineral salt content. This fact must clearly be taken into account in considering its relationship to the plutonic group which I have mentioned. For similar reasons it might perhaps be expected that plutonic species should have close relatives among species occurring in coastal areas. Such affinity is, however, less easy to demonstrate than in the case of desert species or even species whose breeding waters tend to have a high organic content. The best example, such as it is, is perhaps that of *Aedes (Aëdimorphus) natronius* and its close relative *Aedes durbanensis*. The former is one of the most remarkable of African mosquitoes. It is known from the Lake Edward area and from volcanic areas of Abyssinia and the Yemen. In the area of Lake Edward its larvae have been found in warm volcanic pools in water of such a high degree of alkalinity that, according to the finder (personal communication), anyone unwise enough to put his feet in them would rapidly have them flayed. Despite their adaptation to this very rigorous environment larvae have also been found flourishing in fresh-water pools in the same area. *Aedes durbanensis* occurs in coastal areas of Tanganyika, Mozambique and Natal and, surprisingly, at Banana near the mouth of the Congo. It has all the earmarks of a coastal species and its larvae, like those of *Aedes natronius*, have anal papillae of a kind normally associated with breeding in waters with a high mineral content. Nevertheless, it has so far been found, as far as is known, only in fresh-water pools. This species is also known from a number of inland localities in Tanganyika and from Pretoria. The Tanganyika localities (Morogoro, Moshi, Turiani) are all in or near areas of heavy rainfall and one of them (Moshi) is volcanic. Pretoria, however, is not notable in either of these respects and this distribution, like those of the majority of other African mosquitoes, remains for the present unexplained.

Among true coastal species are *Aedes (Aëdimorphus) irritans* and *nigricephalus*, which are West African and indigenous, *Aedes (Diceromyia) adersi*, which is East and South African and indigenous, *Aedes (Skusea) pombaeensis*, the sole representative on the African mainland of this Oriental subgenus, which is East and South African and occurs also, together with at least one other species of the subgenus, in Madagascar, and a number of *Culex*, of which one is East African and indigenous, another both East and West African and

indigenous, a third East and West African and Oriental and a fourth East African, Oriental and Australasian only. Lastly, special mention must be made of the very interesting subgenus *Ochlerotatus* of *Aedes*. This subgenus occurs throughout the Holarctic and along the Andean chain into South America, reappearing in New Zealand, Tasmania and Australia. It scarcely occurs at all in the Oriental region but extends from the Mediterranean down the east side of Africa to the Cape. In North Africa it is represented by *Aedes caspius*, a species of very wide distribution in the Palaearctic Region which extends up the Nile Valley into the Sudan, Eritrea and Arabia. In Eritrea and the Sudan it overlaps with *Aedes caballus*, a species which is known also from Persia and which extends down the east coast and into Cape Province and South-west Africa. This is not, however, a purely coastal species, since it has been found far inland in the Orange Free State, the Transvaal and Southern Rhodesia. *Aedes caspius* is more exclusively coastal but it has been found in several oases in the North African deserts and extends as far up the Nile Valley as Aswan. There are several interesting inland records of this species from Great Britain and I was able to investigate one of these, from the Aldershot area, myself. In this case *Aë. caspius* was found breeding in great numbers in a sewage effluent. Water of this kind is, of course, likely to have a high chloride content and this may well be an important factor in facilitating the inland spread of coastal species. Such species also commonly have a very extensive flight range, as do others associated with desert oases. Special interest also attaches to the recent discovery in Cape Province of two remarkable new *Ochlerotatus*. These show so close a resemblance to Australian species that it is difficult to decide whether they represent the results of variation after introduction or are genuine relics of an ancient 'antarctic' fauna.

The study of the subsequent spread of introduced species could, if initiated at the time of their introduction, throw much light on problems of distribution. No such study has, however, been undertaken in Africa and all that is possible at present is to attempt to reconstruct something of the past history of species which have already become established. The principal vector of urban yellow fever, *Aedes aegypti*, may or may not be African in origin. It belongs to the African group, is now cosmotropical in distribution and has as its only near relatives two remarkable species confined to Mauritius. These species, unlike other *Stegomyia* are very pale in colour and *Aë. aegypti* itself is represented by a pale form which, in Africa, is largely confined to coastal areas and has almost certainly been introduced, probably, in the case of the East African form, from the Red Sea area where it occurs very abundantly. This form has the appearance of a desert mosquito and flourishes particularly in arid regions, but it is also found in areas of high rainfall both on the East African coast and in West Africa, including the island of Sao Thome and in regions as remote from Africa as the West Indies and northern Australia. In Africa south of the Sahara it is found only in ports and in one or two rail or river heads. This affords strong evidence that it has been introduced by man. The problem of why it should remain so purely coastal after introduction remains to be solved. It shows the same restricted distribution in Mauritius and the Seychelles where it appears to form a large, if not the major element in the *Aedes aegypti* population. This species is very easily cultured in the laboratory and would seem to afford ideal material for studies on population genetics.

The common domestic mosquito of the Holarctic, *Culex pipiens*, is represented in Africa south of the Sahara both by the type form and by a subspecies, *C. pipiens* subsp. *fatigans*. The former is largely confined to high altitudes or to high latitudes and this is in accordance with its distribution elsewhere in the world which is largely temperate and subtropical. *C. pipiens fatigans*, on the other hand, is cosmotropical in its distribution. It has only recently been relegated to subspecific status by reason of the fact that it has been shown to

produce naturally occurring hybrids, as well as laboratory hybrids, with *C. pipiens pipiens* in the southern United States and probably also in China and Japan. The male terminalia of the two forms are very distinct but those of the hybrids are intermediate and it is probable that some degree of convergence also takes place in response to climatic conditions, particularly temperature. The extent of this convergence in Africa is being studied at the present time. The type of morphological variation involved is very similar to that described above for *Culex univittatus* but with the added advantage that the character in question can be measured accurately and expressed numerically. The work involved takes much time and only a few preliminary results are at present to hand. These appear to suggest some correlation with temperature, but the picture which eventually emerges is unlikely to be very simple and any generalizations based on the available data might well be misleading. Nor is any experimental evidence at present to hand regarding the influence of variations in temperature during the early stages of development. The possibility and even probability that the East and West African populations of *C. fatigans* are of extraneous origin may also introduce a confusing element. *C. fatigans* is by no means uniformly distributed in Africa. It is much less common in the west than in the east, and there are important differences in behaviour between West and East African forms.

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DISTRIBUTION OF BLOOD PROTOZOA IN AFRICA

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When I rather unguardedly agreed to talk about the distribution of blood protozoa in Africa, I had not properly realized either the scope or complexity of the subject. Up to now in this symposium, speakers have been able to confine themselves to two factors only: the organism and the environment. With the blood protozoa come inevitably two more: host and vector—the protozoon cannot exist apart from its host, and can only survive as a species when accompanied by its vector. Both host and vector are dependent—often in quite different ways—upon the environment. Distribution of the blood protozoa must therefore depend upon the presence of both host and vector—when these are absent obviously the protozoon will be missing, but the contrary does not necessarily apply: i.e. the host and vector may be present, but the protozoon will not always accompany them. If it did, then there would be no zoogeography of blood protozoa—there would merely be the combined zoogeography of host and vector.

The factor of human interference affects the distribution of most of the flora and fauna we have been considering; but in the case of the blood protozoa, this factor is even more important, because it can act separately on the parasite,

host and vector. Man, for instance, may deliberately eradicate a parasite causing harm to himself or his stock by mass treatment with drugs. Or he may unintentionally exterminate the host—say the larger antelopes—by over-running the land in the march of civilization. Or he may abolish the vector, as by mosquito control measures, or inadvertently by changing the environment (e.g. by increasing the density of population, tse-tse flies will be driven away). On the contrary, man may increase the numbers of the host (and thus of the blood protozoon) by domestication or by importation, and increase the vector by providing better breeding places or by transporting it unawares to new places—like *Anopheles gambiae* from tropical Africa to Upper Egypt or Brazil.

Well, what are these blood protozoa in Africa? They belong to two classes only—the flagellates and sporozoa; few genera are concerned, although the number of species is fairly large. They occur in man and his stock, and in wild animals. The wild animals may be migratory or static. All these hosts except the last—the static wild animals—are subject to great interference by natural and artificial factors, and to unravel problems of their zoogeography may be very difficult. The simplest clues are probably provided by parasites of static wild animals, but unfortunately data concerning them are scanty. The best parasites to study would thus be those whose host and vector have a restricted range; a good example would be a haemogregarine of a lizard—a creature which often spends its whole life within a few yards of a single rock; the vector is the equally static ecto-parasitic mite.

The last point I should like to mention in this introduction is the difficulty in identifying species: a few are well known, but many exhibit such variation in structure in the same host—like the bird trypanosomes, or take on such a different appearance in other hosts, that final identification of many of them is still lacking—and of course, as our President has said in his introductory remarks, without exact systematic knowledge zoogeography is impossible.

In a short paper like this, one could either give a summary of existing information, or deal with some special aspects and problems. I propose to do the latter and particularly in reference to the haemosporidia. I shall just mention briefly the trypanosomes and piroplasms, and shall ignore leishmanias, toxoplasms, etc., which are primarily tissue rather than blood parasites. I have also omitted the blood protozoa of fish.

MALARIA PARASITES.

The complex here is the parasite, vertebrate host and mosquito. There are many species of parasite, most of which are vertebrate host specific, but transmissible by more than one species of mosquito. The human parasites are found throughout Africa except in deserts and in places above a certain altitude—which in equatorial regions is about 9,000 feet. There are four species in man, which vary in their distribution. The so-called tropical form *Plasmodium falciparum* is everywhere; likewise quartan, although its distribution is more patchy. This form, due to *P. malariae*, has a reservoir in the chimpanzee. It is never as dominant as *P. falciparum* because (a) the inhabitants quickly acquire an immunity to it, and (b) it is not altogether happy in its insect host—taking a long time to develop and then only to a sparse degree. There are some curious features about the benign tertian malaria parasite (*P. vivax*) in Africa. This is essentially a parasite of temperate zones, and one may travel through vast tracts of tropical Africa without discovering it. Some workers think that the negro is naturally immune to this species: if true, this would explain its rarity. On the other hand, one suddenly comes on small enclaves where many of the inhabitants are infected. There is a village in the Kavirondo plains where the infection rate from *P. vivax* is 24 per cent, whereas in an apparently similar environment

thirty miles away it is nil. Then during an epidemic which raged during the last war in the Chepalungu Forest on the Masai border of Kenya, the infections were largely of this parasite, though in the neighbouring Kericho Highlands—where an epidemic of malaria was also going on—*P. vivax* was absent. *P. vivax* is common in India, and I used to think that these curious localizations of *P. vivax* were due to the presence of recently arrived Indian immigrants, bringing the Indian parasite with them, and initiating a little focus—but this is not always the case. The most interesting example for zoogeography is provided by *P. ovale*. This is an uncommon parasite of man—but it can always be recovered in Lagos and Accra. One meets it very rarely elsewhere in tropical Africa—but why? Man and mosquito are both susceptible and ubiquitous: there must be an unknown extrinsic factor limiting its distribution.

Monkey malaria presents some interesting problems; first in the higher apes—malaria in chimpanzees is confined to a limited part of West Africa, Cameroons, Sierra Leone, Lower Congo, where three species (*P. reichenowi*, *P. schwezi* and *P. malariae*) are common. Travel further east towards the Uganda border and the parasites disappear after Stanleyville, though the chimpanzee is still common. (There is a single record of *P. reichenowi* by Duke from Uganda.) Exactly where and why this disappearance occurs is unknown—the solution lies somewhere in the depths of the Congo Forest. In the lower apes, the situation is much the same: *P. gonderi* is found in mangabeys in the Lower Congo (Léopoldville)—but not as far east as Stanleyville. Experimentally *P. gonderi* will take in many other species of monkey. It was originally found in one of Hagenbeck's circus monkeys in Germany—imported from an unspecified place in the Congo.

The facts concerning the newly discovered parasites (*P. berghei* and *P. vinckei*) of tree rats (*Thamnomys surdaster*) give a neat clue to their distribution. The parasites are capable of infecting many rodents, but are only found in nature in a small locality in galleried forest in the Katanga (Belgian Congo). They are all found here, because apparently only a special species of mosquito, *A. durenii*, is able to transmit them and this mosquito is practically limited in its distribution to this actual locality. *A. durenii* occurs almost nowhere else, so the parasite is confined to the one place. It seems probable that the localization of a newly discovered bat parasite *P. roussetti* may be explicable on a similar basis. This was found in fruit-bats in caves in the Congo—and the Belgian workers think that special cave-dwelling *Anopheles* (*A. rodhaini* and other species) are the vectors.

Malaria parasites of lizards have been less studied than those of other animals, and we know less about the various species and where they are found. This is rather unfortunate, because lizards fulfil some of the best requirements for the study of zoogeography and protozoa: they are stationary in their habits and are fairly unlikely to be transported artificially. *P. pitmani* is found in several species of skink around the shores of Lake Victoria—Hoare found this parasite on the Uganda side of the lake and in the Sesse Islands and I found it on the Kenya, though it is missing in the same species of skink in between and farther south at Mwanza. Farther west in the Congo at Stanleyville, Schwetz found a very similar species in these lizards. To the east, on the shores of the Indian Ocean, the lizards exist but not the parasite. This is an example of typically western fauna finding itself the wrong side of the Divide—probably being left behind in a relict forest. Another species of lizard malaria is found in agamids and *P. agamiae* is widely distributed in Africa: in the Anglo-Egyptian Sudan, around Lake Albert, Lower Congo, Nigeria, Sierra Leone, Liberia and Gambia. The infection is absent in these lizards in the Eastern Congo, Stanleyville, in Uganda and Kenya, and in S.W. Arabia*, also to the north, in Egypt.

* Material from Arabia and Egypt was supplied to the author by the United States Naval Medical Research Unit Number 3.

Malaria parasites of birds are at least as widely distributed as those of man: the migratory habits of birds ensure a widespread dissemination of the parasites, and in the case of birds there is little host specificity. The commonest is the well-known *P. relictum*, which is to be found in many passerine and other birds throughout the continents. A variety of this parasite, var. *spheniscidae*, has been described in penguins from Saldanha Bay, South Africa, and the authors—Fantham and Porter—point out that the same variety is to be found in Patagonia and in Antarctica.

The tiny *P. vaughani* is found wherever surveys are at all extensive. The closely related *P. rouxi* is apparently confined to the North African littoral from Morocco to Egypt and has not been clearly identified farther south.

The most interesting malaria parasite of birds is probably *P. durae*, found in turkeys and limited to a few localities in Kenya. The natural host bird and vector are unknown—very likely details concerning them would clarify the situation. Turkeys are kept in many other parts of Africa, and if the infection were present elsewhere, it would probably have been recognized—*P. durae* produces a disease with dramatic symptoms.

P. fallax provides another interesting example of localization. It was found originally by Schwetz in little owls in Stanleyville and it was rediscovered by the American expedition to the Southern Sudan a few years ago—not in owls but in guinea-fowl. The latter bird has often been examined in other parts of Africa, but *P. fallax* has not been found and it appears that the infection is confined to an area embracing N.E. Congo and Equatoria in the Anglo-Egyptian Sudan.

HAEMOPROTEIDS AND HAEMOGREGARINES.

The Haemoproteidae is another family, closely related to the malaria parasites, which contains three genera, widely distributed in Africa. The genera are *Hepatocystis*, *Haemoproteus* and *Leucocytozoon*.

Hepatocystis. *H.* (= *Plasmodium*) *kochi* is found in the lower monkeys throughout tropical Africa, as far north as Eritrea (in baboons) and as far south as Durban, and at altitudes from sea-level to 6,500 feet on the Equator. It is not found in N. Africa, presumably because the only indigenous monkeys there are macaques, which appear not to be susceptible to this infection. It is strange that the vector of this parasite—about the commonest in Africa—remains unknown. Like certain other flora and fauna, *H. kochi* prefers the margins of forests and second growth forest to the interior of primeval forest, where it is less common.

The epauletted fruit-bats (or flying foxes) of tropical Africa also have a malarial parasite belonging to this genus. It is found in French West Africa, the Congo (from Boma to Stanleyville), the Southern Sudan, and at least as far east as near Nairobi in Kenya. It seems likely that this parasite *H. epomophori* will prove as ubiquitous as *H. kochi*. *Hepatocystis* or a related genus in insectivorous bats, on the other hand, is infrequent and very localized in distribution. Dr. R. B. Heisch has recently found a colony of *Nycteris* bats in caves outside Mombasa highly parasitized. But similar species of bats elsewhere in Africa and in S.W. Arabia show no malaria parasites. There is a single record from Liberia, however, of what seems to be the same organism, and possibly others from Boma and Grahamstown.

The so-called malaria parasite (*P. brodeni*) of the elephant shrew has only been found in the Equatorial Province of the Southern Sudan, and north of Elisabethville in the Belgian Congo, with a doubtful record due east of the latter place in Nyasaland. Elephant shrews have been examined elsewhere but with negative results.

The two common bird parasites *Haemoproteus* and *Leucocytozoon* are at least as widespread as *Plasmodium* in birds, and an even wider range of birds is affected. Species differentiation is still in a primitive state with most of these parasites; certain species like *Haemoproteus columbae* of the pigeon are cosmopolitan. The vector of *Leucocytozoon* is a *Simulium* fly. These flies are apparently absent in lower Egypt and it is interesting to note that the parasite itself does not occur there except scantily in the blood of a few migrants.

Haemoproteus is occasionally found in snakes, and the same species *H. najae* has been found in spitting cobras as far apart as the Sudan and the Gambia.

The reptilia are of rather special interest to our subject; they are very old in the evolutionary scale, their parasites seem to have become stabilized and the present-day distribution is extremely wide. This feature is shown well in the next group of protozoa—the haemogregarines, a composite group belonging to at least five genera and two orders, usually transmitted by leeches in the water forms and by mites or fleas in the land forms. (Haemogregarines are very common parasites of African animals; for the last three years we have been examining the blood of animals dying in the London Zoological Gardens and a total of one-third of all positives in African animals belonged to this group.) A good example is the haemogregarine of the crocodile (*Hepatozoon pettiti*) transmitted by tsetse. This has been found in crocodiles in the Anglo-Egyptian Sudan, Kenya and Uganda, Belgian Congo, Gold Coast, French West Africa and Liberia; haemogregarine cysts were first found (in 1913) in *G. palpalis* by Chatton and Roubaud in the Casamance River in Senegal, and it was not until 1932 that Hoare put two and two together and showed that the cysts in the fly were the sporogonic stages of the haemogregarine of the crocodile.

Haemogregarines of agamid lizards are widespread in the Ethiopian region, particularly in the extreme West (Gambia, Nigeria, Senegal and Lower Congo) and in the extreme East (S.W. Arabia); curiously enough, in between, in the Upper Congo, Anglo-Egyptian Sudan and East Africa, the parasite seems to be absent. I have just returned from East Africa where once again I examined the lizards in Tanganyika and Kenya with negative results.

The specific or even generic identification of most of the haemogregarines of cold-blooded vertebrates is so provisional, that there is little point in discussing them further. *Lankesterella* of frogs however is sufficiently distinctive to mention. This has a cosmopolitan distribution; yet it appears to be absent from the eastern side of Africa, Sudan, East Africa and S.W. Arabia, but it is common in Gambia and the Lower Congo.

Haemogregarines (*Hepatozoon*) infect certain small mammals, rodents, dogs, jackals and hyaenas, particularly in the drier parts of Africa. Thus, *Hepatozoon* is widespread in North Africa and in the Sudan, less common farther south except in rats and mice, though in any given population a small percentage only will be found infected. This is in contrast to the reptilian forms which often show a nearly 100 per cent infection rate.

THE TRYPANOSOMES.

I wish I had time to treat these organisms in detail, because they illustrate many important points. *T. lewisi* is an example of a parasite always found if its host—rats and other allied rodents—is present, and its zoogeography is merely that of the rodent host. *T. lewisi* belongs to the group of trypanosomes developing in the posterior station in the invertebrate; others of this group are ubiquitous also, like *T. theileri* in cattle; the distribution of *T. grayi* of crocodiles is limited to places where its vector occurs, i.e. *G. palpalis* regions (East Africa, Nigeria, Senegal).

The pathogenic trypanosomes transmitted by tsetse are likewise mapped by the distribution of the vectors. A *G. palpalis* map pretty well coincides

with the distribution of *T. gambiense*; a *G. morsitans* with *T. rhodesiense*. This is not entirely so, and in parts of Nigeria there is—as General Vaucel puts it—the paradox of plenty of *G. palpalis*, yet no trypanosomes. Particularly with the eastern form (*rhodesiense*) such dissociation may be explained by the temperature factor—the fly existing, but the parasite unable to develop owing to the low temperature. *T. vivax* and *T. congolense* show much the same relationships with the fly, though the former sometimes escapes and establishes itself in places where tsetse flies are absent, as in Mauritius. The distribution of *T. evansi* is rather strange in that it has practically failed to penetrate into tropical Africa proper—on the east it gets down to the Northern Frontier province of Kenya, on the west to Lake Chad, but it is arrested from further progress south by the Senegal and Niger rivers—which also stopped the Arabs. It appears again as an immigrant in dromedaries in South Africa.

The avian trypanosomes are as widespread as other bird parasites though special methods may be required to demonstrate them. In bats also, they are commonly found when the method of xeno-diagnosis is employed. Trypanosomes are common in lizards and other cold-blooded vertebrates—and one species is found in places as wide apart as the Ivory Coast and Kenya (*T. martini* in skinks).

THE PIROPLASMS.

The last big group of blood protozoa are the piroplasms, of great veterinary importance, and affecting a wide variety of wild animals, including snakes and birds, but for some curious reason, not man. East Coast Fever (due to *Theileria parva*) sounds from its name as though it should possess zoogeographical interest. It is certainly commonest in South Africa, Rhodesia and East Africa, but the infection extends into the Congo and up to Senegal on the West Coast. *T. mutans*—a non-pathogenic species found in cattle—is on the other hand cosmopolitan. The piroplasms of wild, non-migratory animals may provide the most significant features for study. Why, for instance, is the piroplasm (*Echinozoon hoogstraali*) of the rock hyrax confined to a small locality near Torit in the Southern Sudan?—it is absent farther south in Kenya and in North Africa and across the Red Sea in the Yemen. Or why is that very unusual piroplasm *Cytauxoon sylvicaprae* of duikers only found in the Transvaal?; duikers have often been examined elsewhere without finding it, except for doubtful records in Angola and Nyasaland.

The only conclusion I can really draw from this short survey is that in the present state of our knowledge no conclusions are possible. There may be something to be deduced from the absence of the parasite where host and vector are both present and the environment seems suitable. Extraneous features spoil our appreciation of the distribution of most of the human and veterinary protozoa, and I think the best line would be to concentrate on organisms living in static hosts like lizards or possibly in bats which are so rich in protozoal fauna and which are less affected by extrinsic factors.

FILARIAL PARASITES OF MAN

By W. E. KERSHAW.

The general impression that the distribution of animals in Africa is closely related to that of plants in the different vegetative zones has been amply justified, and whilst this may be true in the case of the animals whose relationship with their environment is relatively direct, this association becomes less evident in the case of those animals which have adopted a parasitic mode of life.

It is perhaps in this connection most instructive to consider the extreme case of the parasites such as the filariae—parasites of vertebrates including man, which are dependent for transfer from one definitive host to the next by the agency of biting and blood-sucking flies—which have little or no free living phase in their life cycle and are entirely dependent upon other animals and insects for their maintenance. They are thus buffered throughout their lives from alterations in the external environment.

Each of the filariae has evolved on widely separate lines and has its own definitive host or hosts with more often than not a multiplicity of vectors, all with their own particular habitats and their peculiar inter-relationships. Each parasitic combination thus behaves as a separate entity.

This is a complex situation, for not only may the same suitable detailed habitat be presented for one vector by different vegetative situations but a parasite which may be transmitted by several different vectors has a correspondingly greater range of more varied opportunities.

I propose to illustrate the differing range of these opportunities by considering two human parasites found in West Africa, *Loa loa* and *Acanthocheilonema perstans*, with which we at the Liverpool School of Tropical Medicine, in particular Professor Gordon, have been concerned during the last five years in expeditions to Nigeria and the British Cameroons in connection with the Loiasis Research Scheme of the Colonial Medical Research Council.

L. loa and *A. perstans* are parasites whose adult forms occur in the deeper tissues of man and possibly certain monkeys and whose first stage larvae circulate in the blood stream. The insect vectors in taking a blood-meal ingest the larvae and, after a period of development, transfer them to a further host during a subsequent blood-meal.

L. loa occurs in man and, we believe, in three species of monkeys living in the canopy of the tropical rain-forest. The intermediate hosts are two, possibly three species of *Chrysops*, which breed in certain restricted conditions on the edges of streams in the forest, or in fresh-water swamp. The adult flies are found in the forest canopy and bite monkeys in the trees or man either on the ground when the sparse bean-stick saplings are cleared, or in houses situated on ridges in the mountainous country at the same level as the forest canopy. The canopy is thus intimately concerned with the adult flies, flight and biting habits, indirectly with breeding places, and with the human and monkey populations.

The distribution of this infection is limited to the rain-forest. There is an immediate cut-off in incidence on crossing the rain-forest fringe to the mountain grassland in the British Cameroons. It probably does not occur in mangrove, and in fresh-water swamp little infection is found, though the fly is abundant. This low incidence may be due to the clearing which is usually found near fresh-water swamp in Southern Nigeria, or to the absence of a true canopy.

The infection is very sensitive to interference, since the incidence is depressed by village and town evolution and markedly elevated by the artificial conditions found in mature rubber estates where a low canopy with no ground growth, with nearby breeding places in fresh-water swamp produces an exaggeration of the essential conditions of the rain-forest.

All these factors thus restrict the transference of infection because of the local breeding sites, the habits of the adult fly in the canopy, and the sensitivity of the host-parasite-vector combination to interference.

Acanthocheilonema perstans occurs in man and possibly in the chimpanzee, though in the case of this parasite, we believe man to be his own reservoir.

The vectors (whose parts in the transference of infection have recently been conclusively proved by my colleagues Dr. Hopkins and Mr. Nicholas) are species of *Culicoides*.

C. austeni occurs in the forest, probably in mud or rotting vegetation, and certainly in very large numbers in the stems of rotting banana plants.

C. grahamii (perhaps a less efficient vector when judged by the results of the laboratory experiments) breeds in the banana stems of the plantations and villages in the Southern Cameroons, and probably elsewhere in the rain-forest and in the wet mud of the streams of the mountain grassland area.

Two other species, *C. inornatipennis* and *C. fulvithorax*, perhaps also act as vectors.

Infections with this filaria in the British Cameroons are universal in the rain-forest but are absent in areas of mountain grassland, though one of the vectors, *C. grahamii*, is present in such a situation. There are many factors which may be responsible for its absence in the grasslands, such as a lower temperature, which may inhibit the development of the infective forms in the vector, or the flies may not survive in such a habitat long enough for the infective forms to develop, and to be transmitted.

On the escarpment of the Bauchi Plateau the infection is again universal and we have found this infection in people who have never left Kano in Northern Nigeria.

It is clear then that the filarial parasite *A. perstans* is endemic in two human populations inhabiting two entirely different vegetative zones—one the tropical rain-forest of Southern Nigeria and the other the arid eroded grassland of the Bauchi Plateau, whilst it is absent in the mountain grasslands of the British Cameroons.

From a consideration of these two parasites, therefore, it is clear that the general impression of the correlation between the geographical distribution of the blood-inhabiting filariae and the different vegetative zones can be pressed too far, for in certain of these parasitic combinations the detailed circumstances which may be necessary for their maintenance may be presented by different vegetative zones, and apparently similar situations may differ greatly in their suitability.

Each parasitic combination must therefore be considered as a separate entity, some such as *L. loa* having a close correspondence with vegetative features because of a critical environmental detail, others such as *A. perstans* having little, because of the many dissimilar but equally satisfactory environmental habitats provided by different vegetative zones.

As more knowledge is gained of these parasites and of their hosts and vectors, with their varied habitats and their reactions to each other in combination, we shall understand better the peculiar anomalies in the distribution of these parasitic combinations.

FRESHWATER ORGANISMS

By E. B. WORTHINGTON.

1. THE DISTRIBUTION TO-DAY.

Most problems of distribution can be explained only after a full understanding has been gained of the barriers which prevent one breeding population from intermingling with another breeding population. The barriers to the distribution of aquatic organisms are very different from those affecting terrestrial or aerial organisms which have been the subject of previous communications to this Symposium. Consequently the aquatic regions of Africa do not coincide with the terrestrial regions.

Simplest of all conceptions applying to the aquatic organisms is that they are limited to water, at least for a large part of their life-histories, and therefore

land provides the barriers. On this basis one should be able to divide the continent into its drainage basins, each of which would be one sub-division of the whole from the distribution viewpoint. In fact, however, this concept, although it provides a basis for discussion, breaks down in a number of ways. For example, many of the smaller organisms may be air-borne at some stage of their life-histories and thereby be capable of crossing watersheds. Even fish may become air-borne, as vouched for by anyone who has watched the African fish eagle stooping to its prey, carrying it a distance of some miles, and then dropping it. The original fish may be killed, but if it happened to be a member of the Cichlid family, which contributes so many species to the African fauna, it may very well have been carrying ova or fry in its mouth, and these ova or fry can remain viable for a long time after the parent fish has been removed from the water.

The simple concept of drainage basins as aquatic regions breaks down also in connection with waterfalls and swamps. A waterfall may be an almost complete barrier between two aquatic regions lying within the same drainage basin; such is the case with the Murchison Falls on the Victoria Nile and the Shiré Falls on a tributary of the Zambesi. Other waterfalls are barriers to distribution in the upstream direction but not in the down-stream; while others, such as the Ripon Falls at the outlet of Lake Victoria, are passable upstream only to the most active swimmers. Swamps which are important features of many African water courses have a different effect: although they may contain abundant water, the rapid decay of vegetation in the tropical climate generally reduces the oxygen tension in that water to such a low level that swamps are barriers to the distribution of all aquatic organisms other than those which have some air-breathing device. In some parts of Africa characterized by peneplain topography, the watersheds separating major drainage basins consist partly of swamps. Such is the case along part of the divide between the Congo and the Zambesi systems and doubtless accounts for the fact that, whereas the fish faunas in these two rivers are in general markedly different, a few species which have air-breathing devices exist on both sides of the watershed.

Taking these and other factors into account, we may conclude that some of the drainage basins of Africa are coincident with aquatic regions, but others, such as the Nile, Congo and Zambesi, are divided into more than one region, each characterized by a particular association of species. The present-day boundaries between one aquatic region and another are generally obvious features, such as watersheds or waterfalls, but the basic reasons for the regional differences are to be sought not so much in these features as we see them to-day but in the geological history.

The number and extent of the aquatic regions depend a good deal on the particular group of organisms in which one happens to be most interested. From the viewpoint of an ichthyologist, I suggest that the following ten regions can be recognized, although most of them can be sub-divided.

- (i) *Northern*. This is limited to the waters of Morocco, Algeria, and Tunis, having their origins in the Atlas and related mountains. The aquatic organisms are European rather than African and include, for example, such species as the brown trout which is indigenous nowhere else in the continent.
- (ii) *Nilotic*. This includes the main Nile, the whole of the Blue Nile system, the White Nile system including Lake Albert, but not the other great lakes near the head-waters. It includes also Lake Rudolph, which is a sub-region through loss of an ancient contact to the White Nile via the Sobat River. Lake Tana is another sub-region with a degree of isolation caused by waterfalls and rapids of the Blue Nile.

- (iii) *Congoan*. This region includes the whole Congo drainage basin with the exception of Lake Tanganyika and Lake Kivu. Again, it has sub-divisions associated particularly with Lake Mweru and Lake Bangweulu in the south-east corner of the region. In many respects the Congoan fauna has similarities with the Nilotic.
- (iv) *Western Rivers*. All the rivers west of the Nile and Congo basins and south of the Sahara Desert can be grouped into one region with a number of sub-divisions. They include notably the Niger, with the Lake Tchad basin as a sub-division, the Volta, Gambia and Senegal. Typically, this region contains a rich aquatic fauna and flora showing many similarities to that of the Nilotic and Congoan regions. All three, for example, contain the largest freshwater fish in Africa, the Nile perch, *Lates niloticus*, or its various subspecies.
- (v) *Zambesian*. This region includes the whole Zambesi basin except Lake Nyasa. It likewise has a rich fauna and flora, but lacks a number of genera of fish, such as *Lates*, which are characteristic of the Nilotic, Congoan and Western regions.
- (vi) *Southern Rivers*. South of the Congo and Zambesi basins the rivers flowing to the Atlantic and Indian Oceans can be grouped into one region which is much less rich in genera and species than those mentioned above. The most typical sub-regions are perhaps those of the Orange and Limpopo rivers.
- (vii) *Eastern Rivers*. The series of rivers flowing eastward to the Indian Ocean to the north of the Zambesi basin may be classed together as one region, although each has its own characteristics. The most important are the Rovuma, Pangani, Tana, Juba and Awash. Their flora and fauna are tropical rather than southern but are much less rich in genera and species than the Nilotic, Congoan or Western regions. This region includes a number of closed drainage basins of which that associated with Lake Rukwa is the most important.
- (viii) *Victorian*. This includes Lake Victoria, Lake Kioga and the system of rivers and swamps draining to the Victoria Nile but above the Murchison Falls; also Lakes Edward and George which drain to Lake Albert via the Semliki River, the division between Nilotic and Victorian regions here being the Semliki Rapids; also Lake Kivu which was once part of the Nile system but was ponded by the Mufumbiro volcanoes and now drains southward to Lake Tanganyika and the Congo. The characteristic of the Victorian region is that its fauna contains comparatively few genera, lacking a number of those characteristic of Nilotic, Congoan and Western regions, but a tremendous number of endemic species which have been evolved in this region and nowhere else.
- (ix) *Tanganyikan*. This includes Lake Tanganyika only, with its few tributary rivers. Of the largest tributary, the Ruzizi which drains Lake Kivu, only the lower part below the waterfalls belongs to the Tanganyikan region. The fauna shows a marked contrast to that of the Victorian region in that it is very rich in genera, a number of them being endemic. It has far more endemic genera and species than the Congoan region to which it drains.
- (x) *Nyasan*. This shows certain similarities to the Tanganyikan region in its rich endemic fauna, as one might expect from the fact that Lake Tanganyika and Lake Nyasa are the two deepest lakes in Africa not far apart geographically. In only a few cases, however, are the same species to be found in both. The Nyasan compared with the Zambesian region to which it drains has far more endemic forms.

2. GEOLOGICAL HISTORY.

During the late secondary, tertiary and quaternary epochs, geological and climatic changes have created, broken down and re-created barriers to distribution; certain aquatic regions have been wholly or partly dried up and other areas which are now desert have been inundated. Although up to 25 years ago there had been few efforts to piece together the slender evidence as it then existed, much has been written on the subject since then and every year brings forward new evidence from geology, climatology, palaeontology, archaeology, zoology and botany. The following is an attempt to reconstruct in a few words some of the most important events with particular reference to the origin of the present-day aquatic biology of the three lake regions, the Victorian, Tanganyikan and Nyasan.

The African land mass is one of the most ancient in the world and therefore has been subject to a very long period of erosion leading to the peneplain type of topography. We can imagine that, at a time when the freshwater fauna and flora originated, much of it by invasion from the sea, the continent consisted of an immense ge-anticline or geo-dome with consequent rivers flowing eastward and westward, but the land mass became planed off at the top so that the main rivers were more or less in contact at their sources in a condition which we can see even to-day in certain swampy watersheds. River capture near the headwaters no doubt assisted in contact of fauna and flora. This would account for the necessary assumption that, while separate invasions from the sea no doubt took place, the original freshwater fauna of Africa must have been similar in its various parts. Whether or not we accept the Wegnerian hypothesis of continental drift does not materially affect the picture.

Later came tectonic movements: a warping of the surface of the ge-anticline to form shallow saucer-like depressions, thereby isolating the eastward and westward flowing rivers; the most important of such depressions is represented to-day by the Victorian region. On either side of this depression came the formation of rift valleys, that to the west in which Lake Tanganyika now lies being very much deeper than that to the east. The rifting movements farther south resulted in one main trough now occupied by Lake Nyasa.

These tectonic movements greatly complicated the original drainage system and led to a series of more or less isolated basins and also to a number of lake environments, some shallow, some deep, which immensely increased the opportunities for speciation, on account of the creation of a multiplicity of ecological niches which did not exist in the rivers.

Although the tectonic movements certainly continued over a very long period, and indeed may still be continuing, there was superimposed upon them volcanic activity, of which the most outstanding example has already been mentioned, namely, the eruption of the Mufumbiro mountains as a series of gigantic volcanoes across the western rift valley, with the result that a former tributary of the Nile was ponded into Lake Kivu and its drainage switched to the Congo system. There are many other lesser examples of volcanoes and lava flows having created lakes.

Superimposed on and partly contemporaneous with the above changes came the series of pluvial and inter-pluvial periods, more or less contemporaneous with the temperate glacial and inter-glacial periods. During an early pluvial period we must assume that a substantial part of the Sudan plain was inundated, giving temporary water connections from east to west and accounting for some of the similarities between the Nilotic, Western and Congoan aquatic regions of to-day. Lake Tchad may be a relic of that Sudanese inundation. The desiccation caused by inter-pluvial periods had a different effect. Many of the rivers were, no doubt, reduced to small dimensions, but the larger ones did not disappear entirely and therefore their aquatic flora and fauna survived. In the central depression of the Victorian region, however, I have contended that inter-pluvial desiccation was sufficient to reduce the

waters to a point at which almost the entire original aquatic fauna was obliterated. A subsequent pluvial period provided new, almost tenantless, aquatic environments in the Victorian region where a rapid process of speciation, originally from comparatively few forms, produced the present-day unique aquatic biology.

Inter-pluvial desiccation was not, however, sufficiently intense to dry up the very deep lakes, Tanganyika and Nyasa, although they must have been greatly reduced from their present volumes. The period of isolation of those very deep lakes has therefore been far longer than that of Lake Victoria, which helps to explain the presence of many endemic genera in addition to endemic species. It is a matter for conjecture, moreover, whether an increase of dissolved salts which may have resulted from reduction of volume may in some way be associated with the remarkable marine facies of some elements of the Tanganyikan fauna.

It will be remembered that Moore in 1903, in order to explain the marine-like forms, suggested that Lake Tanganyika represented the relict arm of a Jurassic sea, and that the idea was subsequently discredited by Cunningham. Since then certain other forms, particularly Bryozoa, close relatives of marine species, have been found in Lake Tanganyika, and J. L. Brooks has recently reverted to the possibility of a marine invasion. I am assured, however, by the geologists most competent to express an opinion that there is no geological evidence whatever on which to base ideas of a marine incursion to Lake Tanganyika, and therefore it must be assumed that the lake's entire endemic fauna must have been evolved *in situ*, or at least in inland waters which have been in the past or are to-day directly associated with the lake.

Playing upon the themes outlined above and fitting in the new evidence as it becomes available, many of the detailed problems of distribution become explicable. Thus, within the Nilotic region, the presence of a few endemic forms in Lake Albert and in Lake Rudolph is explained by the fact that only in those two lakes exist the ecological niches of comparatively deep water. Lake Rudolph has produced several subspecies of truly Nilotic forms during its comparatively short period of isolation from the White Nile, a time during which the lake's water has greatly increased in its alkaline content through evaporation in a closed drainage basin. Again, in the Victorian region, the peculiar relationships between the fauna of Lake Edward and that of Lake Victoria are, no doubt, associated with the river reversals which are known to have taken place in the intricate series of sluggish rivers and papyrus swamps which more or less connect the two. The minor but important differences between the fauna of Lake Kioga and of Lake Victoria are explained by the partial isolation between the two, occasioned by the Ripon and Owen Falls and the associated rapids on the upper reaches of the Victoria Nile. Thus the jig-saw of distribution can be filled in, but there is a great deal of further research needed before all the problems can be explained on sound lines.

3. SPECIATION.

This section is very brief because a separate paper going into some detail concerning the fascinating problems involved is being prepared for publication elsewhere. Many problems are connected with the great lakes lying in the Victorian, Tanganyikan, Nyasan and Nilotic regions, and particular interest has centred on the fishes which are better known than the aquatic invertebrates or the aquatic flora.

Since the early Tanganyikan expeditions a number of ichthyologists have contributed to knowledge of the basic facts, notably Boulenger, Regan, Trewavas, Worthington, Poll, and more recently Greenwood and Lowe. Large numbers of species have been described from the various lakes, and

since many were originally known from very few specimens, a number of species have subsequently been discarded, lumped or re-described. New forms will, no doubt, continue to be discovered for many years to come, and a proper understanding of these numerous generic, specific and subspecific differences will gradually come forward as the many different forms are related by field work to their environmental conditions. Meanwhile, the data collected in the field, laboratory and museum by many specialists have been used in general literature on evolution, because these problems of speciation in African lakes certainly have an important contribution to make towards evolutionary biology. Much of the discussion has centred on the problem whether it is necessary to invoke a process of sympatric speciation (speciation in the absence of isolating factors) to explain some of the known facts, or whether all are explicable on allopatric (involving isolation) principles.

Since sympatric speciation in the sense originally used by Ernst Mayr is difficult, if not impossible, to explain on current genetical hypothesis, some contributors to the discussion have stretched the known facts of geology and physiography to breaking point in their endeavours to explain all the speciation on allopatric principles. Certain other arguments have been advanced with a disregard for what is known of the limnological conditions in which the many species are found to-day. A good deal of the argument depends, however, on the precise definition of terms. A species flock may have come into existence within one single lake, and therefore involve sympatric speciation in a broad sense, but within that lake there may be ecological niches of a similar kind, isolated from one another by many miles of aquatic environment which could not be traversed by a species with particular adaptations. Here also comes in the influence of free-roving predators which are always ready to snap up those organisms which stray from the niches to which they are specially adapted. Lake Tanganyika is rich in such predators, Lake Nyasa less so, and the lakes of the Victorian region least of all.

It is sufficient to state here that, by extending ideas of isolation to the minutiae of ecological conditions, nearly all the speciation concerned can be explained on allopatric principles without stretching the imagination too far. There remain, however, certain cases which can hardly be explained on such lines, notably a species flock of small free-ranging predators in the genus *Haplochromis* in Lake Victoria, and it seems necessary that this and similar cases must continue to stand as *prima facie* cases of sympatric speciation until they can be reasonably explained by other means.

4. EFFECT OF MAN ON NATURAL DISTRIBUTION.

Considering the important contribution which the distribution of African aquatic flora and fauna may have to make towards fundamental knowledge of evolution, it is a matter of some concern that human influences may disrupt the natural distribution before it is adequately described and understood. The most obvious way in which these influences work is in moving aquatic organisms, particularly fish, from one region to another and from other continents into Africa, for the sake of economic development and the control of disease. This has, in fact, been going on for a long time: for example, various anomalies in distribution of certain fishes in isolated waters near the East African coast have been attributed to Arab influences dating from centuries past. A more obvious case is the distribution of trout and other sporting fish into the Southern Rivers region and into streams of the mountain areas in nearly all of the other aquatic regions. From the viewpoint of an ichthyologist it is fortunate that the trout have in tropical Africa but a small effect on the indigenous fauna, because in general the lower altitudinal and temperature limit of trout coincides rather closely with the upper limit of the

indigenous fishes. Considering the benefits which trout have brought to many parts of Africa, it would be quite unreasonable to decry the continued development of trout fisheries, provided always that some highland streams remain in their original condition for future hydrobiological study.

More dangerous perhaps from the purely scientific point of view is the modern development of fish-farming in many parts of the continent, based largely on indigenous species of *Tilapia*. Since most of these species are endemic to particular fish regions or sub-regions, it is clearly desirable that knowledge should be gained of the particular attributes of each under domesticated conditions before wide distribution of the most useful species takes place. Some of this knowledge has already been gained. As an example, *Tilapia melanopleura*, a species from the south-eastern corner of the Congoan region, has now found a new home in many fish farms and artificial waters in other parts of the continent on account of its particular attribute of eating aquatic vegetation and grass, which in fish ponds are a danger to human health on account of malaria and bilharziasis. This problem and also the introduction of carp, which has in the past taken place with unsatisfactory results in parts of Africa, have been extensively discussed at recent conferences and symposia of specialists, and can be said to be reasonably under control.

The alteration to Africa's lakes and rivers as a result of hydro-electric schemes and reservoirs is likely to have considerable influence on the natural distribution. As an example, by the end of 1953, Lake Victoria will become the largest reservoir in the world and the partial barrier to distribution between Lake Victoria and Lake Kioga will be replaced by a complete barrier at the Owen Falls Dam. In this case, after careful consideration, it was decided not to insist on a fish pass being incorporated in the construction of the dam. In the case of some other dams, however, on the Nile as well as other major rivers, it is essential for fish passes to be incorporated to allow of economic fishery development.

In the Western Rivers region, which is largely devoid of lake environments, a great African lake is likely to be created in the Gold Coast as a result of the Volta River Project which will inundate a substantial part of that river's basin. This should make fascinating study in seeing how river organisms adapt themselves to the environment of a very large and comparatively deep lake. The adaptability of some of the African fishes in new environments is quite astonishing; among the Cichlid fishes, for example, there is already evidence that some species, when introduced to new environments, alter their habits and even their structure appreciably in a comparatively few generations.

I would conclude these remarks by emphasizing that, while the bare outlines of the problems of distribution of African aquatic organisms are now known, there will be ample material for intensive study by many future generations of hydrobiologists.

THE SPREAD OF AFRICAN TRYPANOSOMES BEYOND THE TSETSE BELT

By CECIL A. HOARE, D.Sc., F.R.S.

An interesting problem in the geographical distribution of blood protozoa is provided by tsetse-borne pathogenic mammalian trypanosomes.

As is known, they are normally restricted to the tropical zone of Africa which coincides with the area of distribution of their intermediate hosts, represented by species of *Glossina*. However, there are some striking exceptions to the rule. Thus, bovine trypanosomiasis due to *Trypanosoma vivax* occurs

not only in certain tsetse-free localities within Africa itself (Belgian Congo, French Sudan, Eritrea, A.-E. Sudan), but has also been introduced with infected cattle to distant lands outside this continent, such as Mauritius, West Indies, Central and South America, where this trypanosome has firmly established itself, in spite of the absence of tsetse flies.

In these countries *T. vivax* is transmitted to cattle mechanically—i.e. without undergoing any development—by horse-flies (Tabanids) and by stable-flies (*Stomoxys*), and it has been demonstrated experimentally that it has lost its power to develop cyclically in its original intermediate host, *Glossina*.

Another example is provided by *T. evansi*, the causative agent of Surra in northern Africa, Asia, and Central and South America. Though this trypanosome is transmitted mechanically by Tabanid flies, it is closely related to the tsetse-borne *T. brucei*, which causes Nagana in domestic animals. Morphologically these two species are almost indistinguishable.

In Africa *T. evansi* occurs chiefly in camels, over an area extending from the Red Sea to the Atlantic Ocean, and southwards as far as 15–16° N. Lat., which is also the northern limit of the tsetse-belt.

There is strong circumstantial evidence that *T. evansi* had originated in the past from *T. brucei*, after the latter was introduced into localities free of tsetse flies, where it was transmitted mechanically by other biting Diptera and ultimately lost its power to develop in *Glossina*. Since the camel has for centuries been the chief transport animal in North Africa, Arabia, Mesopotamia, Persia and parts of Central Asia, it is conceivable that Surra was gradually spread by caravans to camels, horses and cattle throughout southern Asia and the East Indian Archipelago. As regards the New World, it is possible that Surra was first introduced into Central and South America by the Spanish Conquistadores with their chargers.

These examples show how trypanosomes, whose geographical distribution in Africa was originally limited to territories occupied by their normal vectors, were able to extend far and wide beyond their natural boundaries, by adapting themselves to transmission by new insect vectors.

CRITICAL OBSERVATIONS UPON SIWALIK DEER

By AUGUSTO AZZAROLI.

(Communicated by Dr. A. Tindell Hopwood, Sec. L.S.)

(With 7 text-figures.)

Several species of deer have been described from the Siwalik Hills. Unfortunately most of them were originally based on very scanty material, so that they are ill defined. Some confusion in their nomenclature arose later, when more complete fossils were found and were tentatively identified with these species. Furthermore the age of most of the specimens is unknown.

It may be useful to give a critical revision of these species, together with an account of some undescribed fossils I have examined in the British Museum (Natural History).

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Cervus latidens (p. 47, pl. 8, figs. 7, 10), based on two isolated upper molars, characterized by their very large size. Some years later Lydekker removed this species to the genus *Oreas*.

Cervus triplidens (p. 49, pl. 8, figs. 1, 2) was based on a fragment of a right maxilla with M^1 – M^2 . The teeth are hyposodont, with a very strong internal column and slight traces of the cingulum. The enamel is strongly folded on the outer surface. Pilgrim (1913, p. 286) doubtfully placed this species in the fauna of the Middle Siwaliks; he also was in doubt about its generic attribution. According to Brown (1926) this species was probably found in the Upper Siwaliks.

In 1876 Lydekker attributed to this species a fragment of a lower jaw (pl. 8, fig. 5), but in 1884 he identified this specimen as *Cervus sivalensis* (see below). In 1935 Colbert tentatively referred to *C. triplidens* a maxilla from the Pinjor.

Cervus simplicidens (p. 51, pl. 8, fig. 3), based on a fragment of a left maxilla with two molars (M^2 – M^3 according to Lydekker, but more probably M^1 – M^2), is a species of medium size, and rather hypsodont. The teeth bear small internal columns and slight but distinct traces of the cingulum. The inner crescents are acute and their anterior and posterior borders are gently concave. The transverse axes of the two lobes are slightly oblique to the longitudinal axis of the tooth. Lydekker pointed out the close resemblance of these teeth to those of the swamp deer (*Rucervus duvauceli*). In this species the features that distinguish *Cervus simplicidens* are more strongly developed: the inner crescents are more acute and the axes of the two lobes of each tooth are set more obliquely to the longitudinal axis. But the cingulum has disappeared, giving origin to a strong internal column and to a strong anterior inner ridge (fig. 5). This applies also to Schomburgk's deer (*Rucervus schomburgki*), whereas in the tamin (*R. eldi*) the inner crescents are not so sharp and more closely resemble those of *C. simplicidens*; but there is no trace of the cingulum, and the basal column is very strong. Lydekker's drawing does not give an exact idea of the degree of hyposodonty, but it seems that in his type of *C. simplicidens* this character is not so extremely developed as in the living species of *Rucervus*.

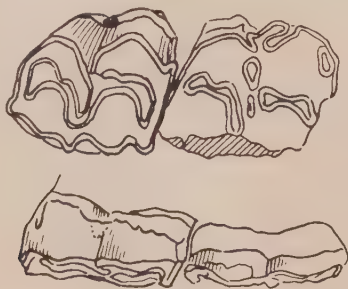


FIG. 1.—‘*Cervus*’ (?) *sivalensis*: Holotype, B.M. 48440. (Natural size.)

Brown (1926) said that this specimen was probably found in the Upper Siwaliks. Pilgrim (1913, p. 285) had put it doubtfully in the Middle Siwaliks.

In 1884 Lydekker attributed to this species another fragment of a maxilla. The identification of this second specimen seems to me very doubtful: the basal column is much more strongly developed than in the type and the **inner** crescents do not show the characteristic acute shape. In 1935 Colbert tentatively attributed to this species a maxilla; this attribution is possibly correct.

Cervus sivalensis was established by Lydekker in 1884 (p. 121). For the holotype he chose a fragment of a left maxilla with M^2 – M^3 . This specimen is preserved in the British Museum (Natural History) and I give here a new drawing of it (fig. 1). To the same species Lydekker referred the fragment of a right

lower jaw he had before (1876) tentatively referred to *Cervus triplidens*. This identification is probably correct. On the contrary, this is not true of his later identifications (1885) and the specimens recorded here are all what is known of the present species. This an unfortunate circumstance, since *C. sivalensis* is a very peculiar species: it strongly differs from any of the other species of deer, living and extinct. The differences are so sharp that I even doubt whether its attribution to the Cervidae is correct.

The type is very much worn, but its most important features are still recognizable. The crown of the upper molars is longitudinally elongated and seems to have been very high. The transverse axes of the two lobes are nearly perpendicular to the longitudinal axis, and the enamel is rugose and strongly folded. There is a strong internal column (not seen in Lydekker's woodcut) and a strong antero-internal fold. These features, with the exception of the rugosity of the enamel, may be considered advanced. On the other hand, there is a continuous, well-developed cingulum, an unmistakably primitive feature.

The lower molars are high crowned; their enamel, too, is strongly folded. The outer crescents are acute and there is a very strong antero-external ridge in the third molar. The transverse axes of the lobes are set perpendicularly to the longitudinal axes of the teeth; and the third lobe of the last molar is well developed.

Another species, *Cervus punjabensis*, described by Brown in 1926, is based on a skull with antlers, from the upper part of the Pinjor. The antlers bear three tines. The skull was badly damaged and has been greatly restored. Brown regarded this species as intermediate between the chital (*Axis axis*) and the sambar (*Rusa unicolor*). As a matter of fact, the material is not sufficient to determine the phyletic position of this species. The antlers are of a rather primitive type, often met with among Pliocene and Pleistocene deer. Their rough similarity to those of the chital and the sambar is no proof of a phyletic relationship. The hypsodont teeth seem to exclude it from the ancestry of the chital, as well as from other more brachyodont living genera (*Cervus*, *Dama*, *Sika*). Brown also pointed out its resemblance to *Cervus simplicidens*. In my opinion the latter is distinguished from *Cervus punjabensis* by the acute shape of the inner crescents of the upper molars.

II.—REVISION OF THE SPECIMENS.

In 1885 some confusion had already arisen, when Lydekker in his Catalogue of fossil Mammals in the British Museum tentatively referred several specimens from the Cautley Collection to *Cervus sivalensis*. Many of these fossils show a marked affinity with the living species of *Rucervus*, but the identification with *Cervus sivalensis* is clearly incorrect.

All the specimens, with the exception of three fragments of antlers (B.M. 41834 b, c, d) show the same state of fossilization. They are pink-brown in colour, smooth in surface and hard. The matrix is very hard grey sandstone. The three fragments of antlers mentioned are more yellow in colour and their surface is a little worn.

The most complete specimen, the greater portion of a male skull (B.M. 39570; fig. 2) shows the same dental characters as *Cervus simplicidens*. This is also true of a fragment of a muzzle (B.M. 17468) in which the teeth are better preserved (fig. 3). The teeth are rather hypsodont, but not so much as in the living species of *Rucervus*.

The skull is of about the same size as that of the swamp deer (*Rucervus duvauceli*) and their morphological characters are very similar. The only difference is that the anterior portion of the muzzle of the fossil species is less elongated. The resemblance to Schomburgk's deer (*Rucervus schomburgki*) and the tamin (*R. eldi*) is still great, but the fossil species is distinguished from the

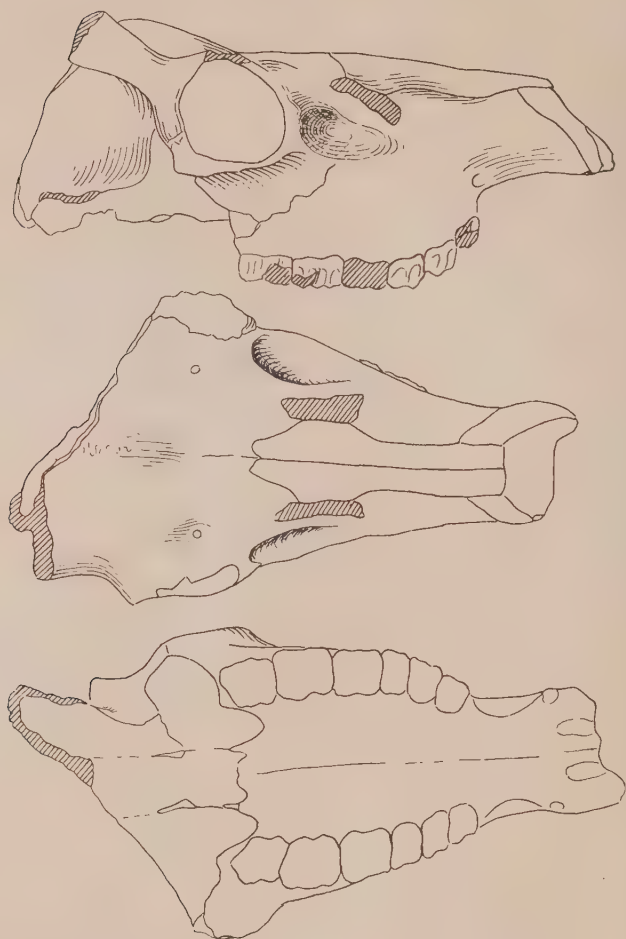


FIG. 2.—*Rucervus* cf. *simplicidens*: Skull, from the Cautley Coll., B.M. 39570. (1/3.)



FIG. 3.—*Rucervus* cf. *simplicidens*: Upper premolars and second upper molar, from the fragment of a muzzle in the Cautley Coll., B.M. 17468. (Natural size.)

former mainly by its more depressed face, and from the latter by the shallowness of the lacrimal pits and the different shape of the nasals. The differences from the other genera of the Cervinae are still greater (cf. Pocock, 1942-44). For these reasons I refer the two specimens recorded above to the genus *Rucervus*. Their identity with Lydekker's *C. simplicidens* is not quite certain, owing to the incompleteness of the holotype, but is very probable. On the other hand, there is good evidence of the affinities of the holotype with *Rucervus*. I therefore propose to call the holotype *Rucervus simplicidens* Lyd. sp., whereas the skull and muzzle of the Cautley Collection may each be named *Rucervus* cf. *simplicidens*.

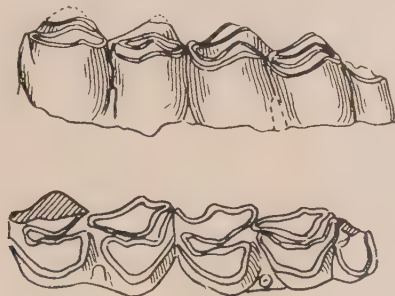


FIG. 4.—*Cervine* ind., fragment of a lower jaw from the Cautley Coll., B.M. M. 16667 (Natural size.)

The state of preservation leads me to suppose that the most part, if not all the specimens listed in Lydekker's catalogue were found in the same horizon as these two fragments of skulls. Several of them might possibly belong to the same species (a fragment of the occipital portion of a female, some fragments of limb bones and several vertebrae), but apart from their size they do not afford any base for identification. On the contrary, a proximal fragment of a radius (B.M. M2311; Lydekker wrongly wrote "distal fragment") is too large for *R. simplicidens* (transverse diameter 64 mm.). A fragment of a lower jaw with M_2 – M_3 (fig. 4) is of about the size that might be expected for *Rucervus simplicidens*, but the rounded form of the outer crescents does not suggest any affinity with *Rucervus*.

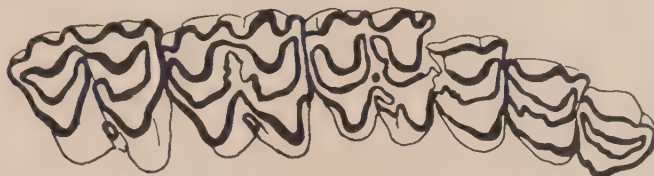


FIG. 5.—*Rucervus dwauceli*: Upper dentition, from a skull in the British Museum, 50.8.30.4. (Natural size.)

The identification of the fragments of antlers is no easier. At least three species are present.

(1) *Rucervus* sp. I (fig. 6).—Two basal fragments (B.M. 41834 b, c) with a strong backward curvature of the beam. These specimens show a very close affinity with *R. eldi*. An upper portion of the beam, very strongly curved (B.M. 41834 d) may also belong to this species. As stated above, the fossilization of these three specimens differs a little from that of the other fossils in the Cautley Collection.

(2) *Rucervus* (?) sp. II (fig. 7).—Two basal fragments, one with a long pedicle (B.M. 41834, 41834 a). They might belong to a species similar to *R. duvauceli*, but are very incomplete.

One of these two species may be identical with *Rucervus* cf. *simplicidens*, and the state of fossilization makes it probable that this is true of *Rucervus* (?) sp. II.



FIG. 6.—*Rucervus* sp. I: Fragment of antlers. (a) Base of a left antler, B.M. 41834 b; (b) base of a left antler, B.M. 41834 c; (c) fragment from the upper portion of a right antler, B.M. 41834 d. From the Cautley Coll. (1/3.)

(3) *Euctenoceros* (?) sp. (fig. 7).—The third species is quite different. It is of a larger size than the others and does not show any similarity to *Rucervus*. The large size and the presence of small tines on the inner side of the first bifurcation vaguely suggest some affinity with *Euctenoceros*.

Two other fragments of antlers are not instructive. One of them (B.M. M. 2308) might be referred indifferently to *Rucervus* sp. I or *Rucervus* (?) sp. II; the second (B.M. M. 15683), collected in the upper part of the Upper Siwaliks or in the Boulder Conglomerate, might perhaps belong to *Euctenoceros* (?) sp. This specimen was found after the publication of Lydekker's Catalogue. In his study on the stratigraphy of the Siwalik Hills, Pilgrim (1913, p. 275) quoted *Cervus* aff. *duvauceli*, found in the upper part of the Upper Siwaliks. It is probable that this species is identical with one of the fossil species of *Rucervus* described above. On p. 325 he included *Cervus sivalensis* in a faunal list of the Upper Siwaliks, but he did not describe his specimens and it is impossible to state whether this identification is correct. Matthew's quotation of *Cervus sivalensis* (1929, p. 444) is evidently derived from Pilgrim's.

Further data on the Siwalik deer were published by Colbert in 1935. The most interesting specimens are an incomplete skull and a well-preserved antler. They were both attributed to *Cervus sivalensis*, but these identifications seem to be based on the data available in Lydekker's catalogue and are wrong.

The antler (A.M. 19807), found in the Pinjor, shows a striking affinity with the swamp deer. It will be called here *Rucervus* sp. III, but is very probably identical with *Rucervus* (?) sp. II. The attribution of it to the genus *Rucervus* may be considered certain.

The skull (A.M. 19829), also from the Pinjor, differs from the type of *Cervus sivalensis* in its dental characters, having but slight traces of the cingulum. It differs, too, from the skull in the Cautley Collection (B.M. 39570) by its larger size and by the rounded shape of the inner crescents of the molars. Apart from the problematic *Euctenoceros* (?) sp., I do not know any species in the Siwaliks with which it might be identified; I therefore propose for it the name '*Cervus* colberti'. The attribution to *Cervus* is provisional, the specimen is too incomplete for closer determination of its affinities. This new species may be diagnosed thus:

'Cervus' colberti, sp. nov.

Diagnosis.—A species of '*Cervus*' which differs from *C. sivalensis* in the slight development of the cingulum, and from *C. simplicidens* by its size, which is larger, and by its teeth which have the inner crescents of the molars more rounded.



FIG. 7.—Basal fragments of antlers. (a) *Euctenoceros* (?) sp., right antler, B.M. M. 2307; (b) *Rucervus* (?) sp. II, left antler, B.M. 41834; (c) *Rucervus* (?) sp. II, right antler, B.M. 41834 a. From the Cautley Coll. (1/3.)

Holotype.—A skull, preserved in the American Museum of Natural History, registered No. 19829.

Horizon.—Lower Pleistocene, Pinjor zone (approximately equivalent to the Villafranchian) of the Siwalik Hills.

Locality.—Punjab, nine miles west of Kalka.

Remarks.—Figured by Colbert, 1935, p. 315, fig. 145.

Two other fragments were tentatively identified by Colbert with *Cervus triplidens* and with *Cervus simplicidens* (see above).

III.—SUMMARY AND CONCLUSIONS.

It is shown in the preceding section that the relationships of the most part of these species, and in some instances even their attribution to the Cervidae, are uncertain. These species are attributed here to the genus *Cervus*, provisionally taken in a very broad sense. Only the species *simplicidens*, whose systematic position is better known, and some isolated antlers, are referred to the genus *Rucervus*. The value of these two generic names is therefore quite different: as a matter of fact, whereas in the Siwalik fauna there are at least two species closely related to the swamp deer and the tamin, the presence of allies of the red deer, of the sambar and of other Cervinae is not demonstrated.

Summarizing the above data we have the following list of species:

'*Cervus*' *triplicidens* Lyd., 1876.—Type: a right maxilla with the first two molars, from the Punjab. Additional specimens: probably a maxilla (Colbert, 1935).

Age of the type, probably Upper Siwaliks; age of Colbert's specimen, Pinjor. Size very large, enamel strongly folded on the outer surface, a very strong internal column.

'*Cervus*' (?) *sivalensis* Lyd., 1884.—Type: a fragment of a left maxilla with the last two molars. Cotype: a right ramus with the last two molars, from the Punjab.

Age not surely known. Size large, teeth hypsodont and complicated, with a strong cingulum in the upper molars. Systematic position very uncertain.

'*Cervus*' *punjabensis* Brown, 1926.—Type: a skull with antlers, from the upper part of the Pinjor two miles west of Chandigarh, Punjab. Medium size, antlers of a rather simple type, with three tines. Teeth rather hypsodont, without inner columns.

'*Cervus*' *colberti*, sp. nov.—Type: an incomplete skull without antlers, from the Upper Siwaliks, nine miles west of Kalka, Punjab. Size large, face narrow and deep, teeth rather simple.

Euctenoceros (?) sp.—A fragment of an antler, of unknown age; possibly also another fragment from the Pinjor or the Boulder Conglomerate.

Rucervus simplicidens Lyd., sp., 1876.—Type: a fragment of a maxilla with M¹-M², probably from the Upper Siwaliks. Additional specimens: none surely identified, but very probably the following specimens: the greater portion of a skull and the anterior part of a muzzle, from the Cautley Collection in the British Museum (Natural History); a right maxilla from the Upper Siwaliks in the American Museum of Natural History (Colbert, 1935). Possibly also other fragments of skulls, limb bones and vertebrae from the Cautley Collection. Skull characters very similar to those of the living *Rucervus duvauceli*; teeth characters also similar to those of the living *Rucervus* but more primitive. Age probably Pinjor.

Rucervus sp. I.—Some fragments of antlers, showing a great similarity to those of *Rucervus eldi*. Probably Pinjor.

Rucervus (?) sp. II.—Some very uncomplete fragments of antlers. Probably Pinjor.

Rucervus sp. III.—A well-preserved antler, showing a great similarity to *Rucervus duvauceli*. Possibly identical with *Rucervus* (?) sp. II. Upper Siwaliks, one mile west of Chandigarh, Punjab.

Probably *Rucervus* (?) sp. II and *Rucervus* sp. III are identical with *Rucervus simplicidens*, but it cannot be excluded that this identity subsists on the contrary between *Rucervus simplicidens* and *Rucervus* sp. I.

In addition, some indeterminable fragments in the Cautley Collection (see above) and the fragment of a skull described by Lydekker, 1884, p. 119, pl. 13, fig. 6 and incorrectly attributed to *Cervus simplicidens*.

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OBITUARY NOTICES

Dr. **William Thomas Calman**, C.B., F.R.S., LL.D. had been a Fellow of the Linnean Society almost continuously for 46 years. During his tenure of office as Zoological Secretary (1923–28) and as President (1934–37) many of our Fellows became aware of his business ability at the Council table, of the wide learning and literary skill that he brought to the editing of our zoological publications, and of the manner in which he could adapt his discourse to the nature of his audience.

I first met him about 1924 at one of MacBride's tea-parties and was invited to call on him at the British Museum. He showed me over his Crustacea section with some pride, since he had recently moved from very cramped to more spacious quarters (which he may have helped to plan). I regarded him with some awe, as a person very much my senior, but shyness was gradually forgotten as this kindly, rather sedate, humorous man, touching on a great variety of subjects, revealed glimpses of his remarkable attainments and forceful personality. "But you don't know your zoology!" (your Shakespeare, your Bible . . . as the case might be) was the prelude to some delightfully apposite remarks. For he had an instinctive sympathy with youth and a firm belief in the value of education as an end in itself. At first it was perhaps a trifle disconcerting to be corrected, albeit in the friendliest way, for the slightest factual or grammatical error; later one learned to appreciate what the late Sir D'Arcy Thompson once called "his singular scientific honesty, an impatience with inaccuracy in any form".

The story of his life is perhaps more characteristic of the nineteenth than of the present century, and of the north than of the south. Of highland descent, he was born (1871) and educated in Dundee, whence his grandfather, a shipbuilder, had moved from the Anstruther district of Fife. His father Thomas Calman, though blind from childhood, was a well-known teacher of music and, as befitted the decades following the Disruption, was keenly interested in controversial theology and in the affairs of the local Free Church. His mother, Agnes Beatts Maclean, must have been a woman of remarkable character; left a widow in very straitened circumstances when her son was six years old, she had to support and educate him and his younger sister on the proceeds of a small millinery business.

Calman's interest in science seems to have awakened very early but it was not until he went to the High School that it received some encouragement and guidance. There he came under the spell of J. B. Charles, who first taught him what literature meant, and of F. W. Young, who had studied under Tyndall, Frankland and Huxley, and whose science laboratory was one of the first, if not the first, in Scottish schools. Meanwhile, a relative gave him a toy microscope and he soon became an enthusiastic student of pond-life. One

source of material was the rich sediment, abundantly populated with micro-organisms, obtained by filtering the domestic tap-water overnight*. From a remark in his first paper (1892) it is clear that he had been familiar with a certain undescribed species of Rotifer from the age of fifteen.

While serving his apprenticeship with the Caledonian Insurance Company he was an active member of the Dundee Working Men's Field Club which flourished at that time. Cyclostyled copies of the club magazine, in his handwriting, show how early his lucid style, his critical faculty and his sense of humour were formed. There he met several men of remarkable character and attainments, including John Hood who shared his interest in Rotifers and who in old age so resembled Darwin*. A power-loom worker who carried a Greek testament daily to the jute mill and "was one of the best field botanists I have ever met" was probably James Fulton. Later he also joined the Dundee Naturalists' Society and became acquainted with Professor D'Arcy Wentworth Thompson who, impressed by his drawings of Rotifers, encouraged him to write his first scientific paper.

Fortunately for zoology, though disappointing for young Calman, his four years' apprenticeship ended with an increase of salary to £30 a year "accompanied by a strong recommendation to take up some other line of business as my stammer unfits me for the insurance profession"†. A timely offer to act as Thompson's laboratory assistant was eagerly accepted and thus began a partnership that was to last for eleven years and lead to a lifelong friendship. Now he was able to study for his degree and three years later (1895) graduated B.Sc. with distinction in Physiology, in Zoology and in Botany, in the University of St. Andrews. Much of his botany he learned from his fellow-student Robert Smith who shared his literary interests and whose early death he was wont to deplore. Then he was appointed Assistant-lecturer and Demonstrator in the Natural History Department, a post which he held until 1903, obtaining his doctorate in 1900. He was a born teacher and on at least three occasions during Thompson's absence abroad was responsible for all the work of the department. He also made himself proficient in several foreign languages.

It may be recalled that Thompson was building up a fine teaching Museum at University College, Dundee. Calman assisted in naming and arranging the rich and varied material received from all parts of the world but chiefly from the Arctic, for the old whaling industry had not then quite come to an end. He described a new genus of compound Ascidians from the Antarctic (1894) and maintained his interest in Rotifers; with Thompson, he encouraged Hood to publish his own discoveries instead of sending his material to Hudson, Gosse or Rousselet. Then he turned his attention chiefly, though by no means exclusively, to the Crustacea and, his exacting teaching duties notwithstanding, published a number of excellent papers. Two are outstanding, namely, those in which he demonstrated with remarkable insight the affinities of the recently discovered *Anaspides* (1896) and of the minute subterranean *Bathynella* (1899, *J. Linn. Soc., Zool.*) with the fossil Syncarida. They attracted the attention of Lankester, whose 'Treatise' volumes were beginning to appear, and Calman was invited to write the Crustacea part (21 September 1901). As originally planned Pocock was to take the Trilobites, Pycnogons and Limuloids with the Arachnida and it is amusing to read that Lankester wanted the volume to go to press if possible by the end of 1902!

This was another turning point in his career. Whereas in May 1901 he had written to D'Arcy "upon the whole, the B.M. offer (if it does come) does

* Hood listed 35 species of Rotifers from this source—see *Scots Mag.*, 1939, pp. 409–418. A portrait of Hood illustrates this biographical essay (*in Scots Mag.*).

† This was apparently due to suppressed left-handedness. When he was past 50 an attack of writers' cramp in his right hand forced him to learn to write with his left one; this he found surprisingly easy, and in a year or two his stammer disappeared.

not promise to be so very tempting", in 1903 he accepted a temporary post at the British Museum (Nat. Hist.) because there he could best prepare the text-book. The following year Pocock resigned and Calman was placed in charge of the Crustacea and Pycnogonida, and for a short time was responsible for the Arachnida as well. In addition to his official duties he for many years compiled the Crustacea and Arachnida sections of the *Zoological Record*. In 1921, the year in which he was elected to the Royal Society, he became Deputy Keeper of the Department of Zoology, and in 1927 he succeeded Regan as Keeper. He retired in 1936; in the previous year he had been created a C.B. and in 1937 was elected an honorary F.R.S. Edinburgh.

As a Museum curator Calman kept the collections under his care in excellent order with the minimum of cataloguing and indexing. From 1904 onwards, until administrative duties claimed most of his time, he also produced a steady stream of scientific papers of the highest order, many illustrated with his own excellent drawings. To a remarkably retentive memory (which enabled him to dispense with card-indexes and even, for the most part, with notes) was added a gift for winnowing the significant from masses of detail. That he handled theoretical questions with wise caution and sound judgment is evident to anyone who reads his presidential addresses, entitled *The Meaning of Biological Classification* and *The Origin of Insects*, delivered to the Linnean Society in 1935 and 1936. As a systematist, to quote his own words, he aimed at "a natural classification that does violence to none of the conclusions of morphology or of palaeontology, and that is consistent with an evolutionary history in which convergence may have played an important part but never the dominant one".

The Crustacea volume in Lankester's *A Treatise on Zoology* appeared in 1909 and if he had written nothing else he would still deserve to be remembered as a great zoologist. The new classification of the subclass Malacostraca, introduced as a preliminary paper in 1904, was based on that foreshadowed by Hansen and others, but only one with insight and vision could have perfected it (as far as our incomplete knowledge allowed). The terms which he proposed for large divisions analogous to the Syncarida, namely, Peracarida, Eucarida and Hoplocarida, and the diagram of a generalized type of Malacostraca showing the 'caridoid facies' are now known to every student. The book is still the best introduction to the Crustacea and may well be the last by a single author; at any rate the more recent German text-books are composite works.

Much of interest that was unsuited to a text-book is included in his more popular book *The Life of Crustacea* (1911). For, although he was primarily a morphologist, Calman was particularly interested in the habits and habitats of the animals that he studied. For example, he was the first to observe that certain quite well-known species of West African river-crabs possess what he took to be stridulating-organs of a type not hitherto known in any other Crustaceans (1908). He could not, of course, prove that these crabs were capable of producing sounds by rubbing the bases of some of their legs against the lower margin of the gill-cover. Thirty years later, however, a correspondent wrote to the Museum asking if we knew of a fresh-water crab in certain forests of Sierra Leone "which emits a piercing whistle at frequent intervals, audible at some distance. The first time I heard it I thought it was made by a bird, but the natives assured me (though I never succeeded in catching one) that it was made by a crab".

His other publications are of more specialized interest but a glance through the long list shows that certain themes predominated. Several papers dealt with rare and interesting deep-sea Cirripedes and Decapods found growing on, or clinging to, submarine telegraph cables when brought up for repair. He described a number of interesting subterranean Crustacea such as the blind Palaemonid prawn *Typhlocaris* from Tiberias. To him we owe our

knowledge of the many endemic species of Atyid prawns peculiar to Lake Tanganyika; these he thought could not belong to the 'halolimnic' fauna of the lake, "but were, rather, the result of divergent evolution and specialization during a long period when the lake was quite isolated". In a critical essay entitled 'The Researches of Bouvier and Bordage on Mutations in Crustacea of the Family Atyidae' he expressed the view that, should later work confirm Bouvier's mutation hypothesis, the Tanganyikan genus *Atyella* may have originated from *Caridella* by a parallel mutation. In 1910 no one suspected that certain Decapod Crustacea, such as *Pandalus* for example, are protandrous hermaphrodites and there is reason to suppose that Bouvier was baffled by cases of sex reversal in the Atyidae.

For a time he served as scientific adviser to a Committee of the Institution of Civil Engineers and made a special study of marine boring animals injurious to submerged structures. This involved work on groups other than the Crustacea and the taxonomy of the shipworms (Mollusca) was particularly difficult. His report for this Committee (1920) and the pamphlet on this subject which appeared in the *B.M. Economic Series* in 1919 were well reviewed. A second edition of the pamphlet, brought up to date by G. I. Crawford (1936), is out of print and Calman's exhibit illustrating the natural history and destructive habits of these boring animals has been dismantled.

The Pycnogonida also claimed his attention and he was thrilled when the fine specimen of *Dodecolopoda mawsoni* arrived at the Museum. He upheld the view that the few decapodous species were not primitive but "rather due to the development of instability of metameric pattern of the normal octopodous forms; and that this had occurred independently in at least three separate lines of descent". *Dodecolopoda* merely carried this one stage further.

The 'Leitmotiv', however, derives from his early interest in *Anaspides* and *Bathynella* and was concerned with the elucidation of the more obscure orders of the Malacostraca and with the phylogeny of the Arthropoda. To him we owe our present knowledge of the Syncarida, fossil as well as recent. As the result of many years' work on the curious, rather primitive members of the order Cumacea, he arrived at a natural classification of the group and the British Museum collection, enriched by many genera and species, became in this respect one of the finest in the world. An eminent authority on the Trilobita writes, "from his early studies on *Anaspides* Calman developed a lasting interest in the nature of primitive Arthropods and in the phylogeny of Arthropods generally. He fostered this in two ways, by carefully describing the morphology of late Palaeozoic Crustacea and by writing thoughtfully critical reviews of others' descriptive and deductive accounts of trilobite appendages. In the first category, he wrote five short papers on Carboniferous Crustacea interpreting several structures in these fossils previously unrecorded, and, jointly with D. J. Scourfield, he wrote in 1919 a preliminary account of the Rhynie Chert (Old Red Sandstone) Crustacea. Elsewhere, in the same year, he suggested that the supposed 'setiferous exopodites' of the trilobite might throw light on the origin of the 'gill-books' of *Limulus*. But when, later, this suggestion had been developed by L. Størmer into an argument to refer the Trilobita closer to the Arachnida than Calman wished, Størmer was criticized (1939) almost as heavily as Walcott and Raymond had been some years earlier for referring the Trilobites to the Crustacea. Well versed in the pitfalls of convergent evolution, Calman held the view that Trilobita stood close to the common ancestors of Arachnida and Crustacea, but belonged to neither group, a view held by many today.

Calman also took a prominent part in scientific activities outside the Museum. He was a member of the Board of Studies in Zoology of London University and delivered advance courses of lectures to students at Bedford College, University College and the Imperial College of Science; he also served as External

Examiner to many Universities in Scotland and England. He was for several years Honorary Secretary of the Challenger Society and Secretary to the Ray Society from 1919 to 1946, during which time he edited the monographs. He served on the Council of the Royal Society (1933-35) and was at various times a member of the Finance and of the Publication Committees of the Zoological Society. Those who served with him on various committees valued his sound judgment and the pleasant and friendly way in which he handled questions over which there was difference of opinion. He was President of the Quekett Microscopical Club from 1927 to 1929 and of Section D at the Bristol meeting of the British Association in 1930. At the time of his death he was an editor of the *Annals and Magazine of Natural History*, a Vice-President of the Marine Biological Association and a member of the International Commission on Zoological Nomenclature. He had long been an Honorary Foreign Correspondent of the Zoological Survey of India and in 1938 was elected an Honorary Member of the Société Zoologique de France.

Apart from his professional life Calman was essentially a family man. His devoted partner during forty-six years of happy married life was Alice Jean Donaldson of Tayport, Fife. A great grand-niece of the distinguished surgeon Sir James Wylie (1768-1854), she was one of the first women graduates in medicine of the University of St. Andrews and in due course their daughter and their son also became doctors. Their home was a centre of gracious hospitality to friends and scientific colleagues of many nationalities. It was a fitting tribute to his wife and to his mother that his views on the position of women were in advance of his time and that he was largely instrumental in getting women admitted to the staff of the Museum.

After he retired he worked for a time at the Museum on the Pycnogonida and the Caridea of the 'John Murray' Expedition (1938 and 1939). Then he moved to Tayport and soon we find him acting as a temporary war-time lecturer in Zoology in his own Alma Mater, of which he was an LL.D. (1937). A series of lectures delivered to his students on *The Classification of Animals* appeared in book form in 1949. The Field Club had long ceased to exist but he resumed his connection with the Dundee Naturalists' Society, being President for the session 1944-45. In the following year he had a serious illness, from which he made a remarkable recovery, although it left him physically weakened. When he came south to receive the Linnean Gold Medal in 1949 a dinner was held in his honour at Birkbeck College. The last two years of his life were spent for health reasons in London and he continued to visit old friends at the Museum, accompanied on occasion by one of his grandchildren. The last time I visited him I thought, as he talked with enthusiasm of the rare trees and shrubs in the fine grounds at Coulsdon, Surrey, that with the years he had changed extraordinarily little. He died suddenly on 29 September 1952, in his eighty-first year.

As administrator of a large museum department he was always approachable and won the respect of his subordinates. To the members of his scientific staff, as also to the students that were sent to him from time to time for help and advice, he gave freely of his time, knowledge and experience. If as editor and administrator he set a very high standard, it was no more than he always demanded of himself and his strictness was tempered by his humorous common sense. All who knew him appreciated his profound erudition, his great personal charm, his modesty, his generosity, and above all his integrity. His memory is held in affectionate esteem by all who came under his influence.

I wish to express my thanks to all those who have assisted me in the preparation of this notice, especially to Professor Peacock and Miss D'Arcy Thompson for copies of documents and letters relating to Dr. Calman's early Dundee period, and to Dr. Roy Calman for access to some personal records.

I. GORDON.

Lt.-Col. **Leonard Charles Rudolf Messel**, O.B.E., M.A., F.L.S., V.M.H. who died at his home in Sussex on 2 February 1953 at the age of 80, was a distinguished horticulturist who became a Fellow of the Linnean Society in 1931.

He was educated at Eton and Merton College, Oxford, and then entered his father's firm in the City and later inherited from him the property of Nymans near Handcross in Sussex. Mr. Messel senior had laid out the garden and had planted in the early part of the century many of the new shrubs and plants introduced by Wilson, Forrest and other collectors from China as well as many beautiful shrubs from Chile and from the more temperate parts of South America. Lt.-Col. Messel continued this tradition by planting in his turn the new introductions of Kingdon Ward and later collectors, besides making a fine collection of *Rhododendron* species and hybrids which became one of the outstanding features of the garden. Here also were grown many of the South American plants collected by Mr. H. F. Comber, son of Mr. Comber the well-known and capable head-gardener who had had charge of the Nymans garden from the time of Mr. Messel senior. Two of the most outstanding Chilean plants were the Eucryphias, the deciduous species *E. glutinosa* and the evergreen species *E. cordifolia*. Both shrubs grew into large plants, growing next to each other, and during the first world war seedlings sprang up around them. These proved to be natural hybrids between the two species and were named *Eucryphia* 'Nymansay'. It is covered with white flowers in late summer and has been found to be just as beautiful as its parents and easier to grow than either of them. It received an Award of Merit from the R.H.S.

Lt.-Col. Messel had inherited with the garden a house of Victorian appearance. He rebuilt it, bit by bit, with loving care, using old and weather-worn stone; he filled it with fine furniture, rugs, tapestries, pictures and objets d'art of all kinds. He had one of the best private collections of botanical and gardening books including many of the finest editions of the old Herbals. In this he was much helped by the enthusiasm and expert knowledge of Mrs. Messel who was a daughter of Linley Sambourne the artist. The creation of Nymans as a beautiful house, full of treasures, in a perfect garden setting was indeed the work of his life-time and it was truly a tragedy when the house with all its priceless contents was totally destroyed by fire in 1947. Although he bore this loss with great courage Lt.-Col. Messel never really recovered from the shock.

Lt.-Col. Messel served on the Council of the Royal Horticultural Society from 1936 to 1941 and was awarded the Victoria Medal of Honour by the R.H.S. for his work as a keen amateur gardener, introducer and grower of rare plants.

He left a widow, two sons and a daughter.

F. C. STERN.

The Danish zoologist Dr. **Theodor Mortensen**, who died at Copenhagen on 3 April 1952 at the age of eighty-four, was well known as the author of 'A Monograph of the Echinoidea', a monumental work published between 1928 and 1951. He was not only a leading authority on the Echinodermata but also a great collector and field naturalist. In the course of his extensive travels he had visited most of the Museums and Marine Laboratories of the world and was thus personally acquainted with many biologists outside his own special field.

Ole Theodor Jensen Mortensen, the son of a schoolmaster, was born at Harløse on 22 February 1868 and educated at Frederiksborg Grammar School and the University of Copenhagen. To please his family he graduated first in theology (1890); his real interest, however, was in natural history, which he taught for a time at the Institution for the Blind while studying for his science degree. Then, for a year he was assistant under Spengel at the Zoological Institute, Giessen, where he commenced his study of the Echinoderm larvae

of the German Plankton Expedition. For the next two years he was assistant at the Danish Biological Station and published several papers on the biology and conservation of food fishes and on the habits and development of the prawn *Leander squilla*. He graduated M.Sc. in 1895 and D.Phil. in 1897. He was associated with the Zoological Laboratory of the University of Copenhagen from 1902 to 1910 and then with the Zoological Museum, where he was Head of the Invertebrate Division from 1917 to 1933.

Mortensen's long life was one of intense productivity. Between 1893 and 1952 he published numerous scientific memoirs, handbooks and monographs. These deal chiefly, though by no means exclusively, with the systematics and embryology of the Echinoderms and their value is enhanced by the excellence of the drawings, all by his own hand, which illustrate them. He was also interested in the habits and habitats of the Echinoderms and in the organisms that live in association with them as commensals or parasites. In 1906 he launched the *Danmark's Fauna* series of Handbooks, which he edited until 1913. When his own volume on the 'Pighude' or Echinoderms appeared in 1924 he was invited to translate it into English. But, since the British fauna is richer than the Danish one, especially in deep-water forms, he enlarged it into 'A Handbook of the Echinoderms of the British Isles' (1927).

He also did some excellent work on Ctenophores; for example, it is to him that we owe our knowledge of the remarkable, sessile, viviparous *Tjalfiella* which grows on the Sea-pen *Umbellula*. At the Dundee meeting of the British Association in 1912 he supported the theory that Ctenophores are more nearly allied to Platyhelminths, such as Polyclads, than to the Coelenterata.

His career is remarkable for the number and importance of his scientific expeditions. These he often undertook alone, with the minimum of equipment, much of which he had made himself or perfected, doing his own collecting and improvising his own primitive 'laboratories' when no proper facilities were available. He led the Danish Expedition to the Gulf of Siam (1899-1900) and the richness of the material obtained in four months testifies to his zeal and ability as a collector. Then, in 1905-06, accompanied by the botanist F. Børgesen, he visited the Danish West Indies where he hoped that a Marine Station might be established. His most extensive expedition was undertaken during the first world war, when he spent two years in the Pacific region, visiting the Philippines, Japan, Australia, New Zealand, Auckland-Campbell Islands, Hawaii, Nanaimo, La Jolla, Panama and Trinidad. Many specialists collaborated in determining the material and some 76 papers have appeared to date in the series entitled 'Papers from Dr. Th. Mortensen's Pacific Expedition, 1914-16'. Before embarking on this expedition he spent some time at the Plymouth Marine Laboratory, studying the development of some British Echinoderms in order to master the latest technique for rearing the larvae (1913). In addition to his general collecting, therefore, he attempted, with varying degrees of success, to rear the larvae of many tropical species of Echinoderms; he even succeeded in transporting alive some larvae from the West Indies via New York to Copenhagen! (see 'Studies of the Development and Larval Forms of Echinoderms', 1921).

After the war, he reverted to the question of a tropical Marine Laboratory and it seemed as if the necessary funds for such a project might be forthcoming. But first a suitable site had to be selected and, with this end in view, he spent a year exploring Amboina, Java, Banda and Kei Islands. Like Max Weber and others before him, he was impressed by the richness of the Kei Island fauna. He found that islands of volcanic origin, such as Amboina and Banda, were quite unsuitable for his embryological work, whereas at the Kei Islands, which are non-volcanic, his cultures were particularly successful even without laboratory facilities. He attended the Fourth Pacific Science Congress in Java in 1929 and submitted his "proposal of establishing a marine laboratory at

the Kei Islands, particularly for the study of the biology of the deep-sea". But by this time he knew that the money would not be forthcoming and that, during his own lifetime at least, the project would remain 'a beautiful dream'. He returned from Java by way of Mauritius, South Africa, St. Helena and the Canaries.

Meanwhile he had embarked on the gigantic task of monographing the Echinoidea or Sea-urchins. The first large volumes were published at the expense of the Carlsberg Fund in 1928, when he was sixty years old. The authorities of the Zoological Museum co-operated by freeing him from all other commitments, so that even before he retired he was able to devote himself entirely to research connected with the Monograph. The satisfaction of seeing the sixteenth and last volume through the press was clouded by anxiety over his wife, who was suffering from a distressing illness. She had shared his life for fifty years and, though she might jokingly remark that she ought to have been a Sea-urchin, she understood, and sympathized with, his whole-hearted, single-minded devotion to his work. His own strength was ebbing and he did not long survive her.

I am not in a position to appraise his contribution to our knowledge of the Echinodermata and for this the reader is referred to the excellent short tribute that appeared in *Nature* for 21 June 1952. From personal experience I know how helpful and encouraging he was to young research students; in the summer of 1926, when I was working at Woods Hole, he travelled a considerable distance, at some personal inconvenience, to inform me of conditions at Bermuda. Anyone else would have sent a letter instead.

He was a frequent visitor to this country, to which he was much attached. He often attended meetings of the British Association, and to the British Museum he rendered invaluable service at a time when there was no Echinoderm specialist on its staff. He was elected a Foreign Member of the Linnean Society of London in 1929 and in 1951 was awarded the Linnean Gold Medal in recognition of his signal service to the science of zoology.

In him Denmark has lost one of a long line of distinguished zoologists that has placed the Zoological Museum of Copenhagen in the forefront of the museums of the world.

I. GORDON.

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